University of Alberta

Stable Isotope Analysis and the Investigation of the Migrations and Dispersal of Peregrine Falcons (*Falco peregrinus*) and Burrowing Owls (*Athene cunicularia hypugaea)*

by

Jason M. Duxbury ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the
requirements for the degree of Doctor of Philosophy

in

Conservation Biology

Department of Renewable Resources

Edmonton, Alberta

Spring 2004

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-96259-8
Our file Notre référence
ISBN: 0-612-96259-8

The author has granted a non-exclusive license allowing the Library and Archives Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou aturement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Abstract

The study of migration leads to comprehension of the connectivity between a species and its ecological requirements in different regions. To understand migration patterns is important since many animals spend significant amounts of time in geographically and potentially ecologically different areas. If conservation and management of Peregrine Falcons (*Falco peregrinus*) and Burrowing Owls (*Athene cunicularia hypugaea*) are to be successful, the population dynamics during a complete annual life cycle of these species need to be understood.

Sample sizes are limited with bird banding due to low recovery rates and with radio/satellite tracking due to the requirement of substantial resources. Traditional methods of tracking migrants have been effective in providing information about migrant birds, but the information can take decades to accumulate. The frustrations of low recovery rates associated with standard migration tracking techniques are being alleviated by new or improved techniques such as stable-isotope analysis (SIA).

SIA provides a method to trace migratory birds without them having been previously banded. Herein, SIA was used to determine the origin of Peregrine Falcons migrating along the Gulf Coast of Texas, and of Burrowing Owls wintering in central Mexico and southern Texas. SIA was also used to determine the scale of inter-year dispersal of Burrowing Owls.

Only 10% of migrant Peregrine Falcons were estimated to originate east of 102° W. The majority of the falcons were estimated to have originated in the western Arctic. Most of the Burrowing Owls wintering in central Mexico appear to be short-distant migrants. SIA established five links between Mexico and Canada and two more feather samples had values consistent with regions adjacent to the Canadian border. Finally, SIA demonstrated that many

Burrowing Owls relocate >500 km between breeding seasons. Dispersal between populations in Canada and the adjacent US states is leading to a net loss of Burrowing Owls from Canada to the US.

Currently, SIA cannot replace the precision of band recoveries or transmitter relocations. However, since birds analyzed for stable-isotope signatures equate to band recoveries in terms making links between two locations, large amounts of data can be collected in a few years instead of decades.

To stop and smell the roses brings happiness.
To stop and pick up a feather brings data and happiness.

Acknowledgements

The first acknowledgments must go to those that volunteered to collect feathers since 1995. Without your interest, I would have feathers from a very limited area of western Canada instead of an area ranging from Alaska to central Mexico and from California to New Brunswick. Thanks to those that collected Peregrine Falcon feathers; G. Holroyd, S. Ambrose, D. Mossop, K. Hodson, C. Shank, M. Bradley, J. Dixon, G. Court, D. Stepnisky, L. Priestley, J. Folinsbee, W. Nelson, P. Thompson, L. Oliphant, R. Jones, B. Ratcliff, T. Armstrong, M. LePage, and B. Mattox, A. Grøngaard, J. Pagel, M. Martell, D. Amirault, and P. Hunter. I recognize that many eyries are difficult to approach and your efforts are truly appreciated. I also thank those who wandered the grasslands in search of Burrowing Owl feathers; G. Holroyd, H. Trefry, D. Shyry, R. Sissons, D. Scobie, R. Russell, D. Todd, R. Poulin, P. Bartels, J. Belthoff, R. Griebel, D. Rosenberg, L. Trulio, J. Barclay, P. Delevoryas, G. Proudfoot, G. Batey, N. Korfanta, E. Valdez, C. Conway, J. Everett, M. Robbins, J. Sleno, P. Arrowood, and M.K. Skoruppa. My sincerest apologies if I have missed anyone.

I would also like to thank the organizations that have supported my stable-isotope projects over the years. Thanks to the Canadian Wildlife Service (especially G. Holroyd) for many years of financial and logistical support and for seeing my projects through from start to finish. I am truly grateful for the Alberta Sports, Recreation, Parks and Wildlife Foundation; the Natural Sciences and Engineering Research Council of Canada; the National Fish and Wildlife Fund (US); and the University of Alberta for believing in the potential of stable-isotope analysis.

I will always be grateful to the members of my supervisory committee; J. Beck for his always-available support at the university, K. Muehlenbachs for sharing his wealth of knowledge of stable-isotope analysis (plus lab space), and for G. Holroyd for his years of support, mentorship and friendship. I am grateful to M.K. Skoruppa for taking the time to organize and ship feather collections from all over the US. Thanks also to H. Trefry for not only help with permits and collecting feathers, but for hours of good conversation and your ability to find good Blue's bars in conference cities. Thanks also to my hard working lab assistants; Mark Wendlandt, Lisa Priestley and Dawn Birn.

Finally, I would like to thank my family (both original and by law) for your unfaltering support over the years. I am and will always be especially grateful to my wife Sandra. Without providing me with the time and support I needed to keep plugging away at my work, I would have never been able to finish. Thank you, SS.

Table of Contents

CHAPTER ONE: Introductory chapter **1**

LITERATURE CITED **10**

CHAPTER TWO: Changes in hydrogen isotope ratios in sequential plumage stages **15**

METHODS **19**
  Quails **20**
  Falcons **20**

RESULTS **23**
  Quails **23**
  Falcons **24**

DISCUSSION **25**

TABLES **28**

FIGURES **31**

LITERATURE CITED **35**

CHAPTER THREE: Remote monitoring of Peregrine Falcons with stable-isotope analysis of hydrogen, carbon and nitrogen ratios in feathers **39**

METHODS **44**
  Sample Collection - Nestlings **44**
  Sample Collection - Migrants **45**
  Feather Analyses **45**
    Hydrogen **45**
    Carbon and Nitrogen **47**
  Statistical Analyses **47**

RESULTS **48**
  Natal Feather Analyses **48**
  Migrant Tracking **51**

DISCUSSION **52**
  Peregrine Falcon Monitoring **55**
  Other Migration Routes **57**

TABLES 60

FIGURES 66

LITERATURE CITED 70

CHAPTER FOUR: Summer origins of Burrowing Owls wintering in Southern Texas and Central Mexico as determined by stable-isotope analysis 76

METHODS 80
  Feathers for reference dataset 80
  Feathers from wintering Burrowing Owls 81
  Tests of Confidence 82
  Feather Analyses 82
    Hydrogen 82
    Carbon and Nitrogen 84
  Data Analyses 84

RESULTS 86
  Isotope Reference Data-set 86
  Migrant Tracking 88
    Long-distance Migrants 90

DISCUSSION 91

Future Research 95

TABLES 98

FIGURES 105

LITERATURE CITED 111

CHAPTER FIVE: Large-scale dispersal dynamics of Burrowing Owls as determined by stable-isotope analysis 116

METHODS 126
  Nestling Feather Dataset 126
  After-hatch-year Burrowing Owl Feathers 127
  Tests of Confidence 127
  Feather Analyses 128
    Hydrogen 128
    Carbon and Nitrogen 129
  Statistical Analyses 130
  Trans-border dispersal and exchange 131

RESULTS 133
Isotope Reference Data-set 133
Inter-Regional Movements 135
Alberta 135
Saskatchewan 135
Montana 136
Wyoming / North Dakota 136
Trans-border dispersal and exchange 137

DISCUSSION 140
Long-Distance Dispersal 140
Inter-regional dispersal and "short-stopping" 142
Trans-border dispersal and exchange 144
Dispersal and Habitat 146
Burrowing Owl Dispersal 147

FIGURES 157

LITERATURE CITED 167

CHAPTER SIX: Discussion and conclusions 181
Summary of Results 182
Future Research 186

FIGURES 190

LITERATURE CITED 191

APPENDIX A: Stable-isotope nomenclature 193

APPENDIX B: Hydrogen isotope patterns across North America 194

List of Tables

Table 2-l. Results from hydrogen isotope analyses of feed and water used in the diet switch experiment involving Japanese Quail...........29

Table 2-2. Feather length comparisons between control and treatment groups of Peregrine Falcons and Japanese Quail..........................29

Table 2-3. Hydrogen isotope analyses of Japanese Quail feathers. 30

Table 2-4. Hydrogen isotope analyses of Peregrine Falcon feathers................31

Table 3-1. Collection sites for nestling Peregrine Falcon feather samples 60

Table 3-2. The isotopic delineation of Peregrine Falcon collection areas across study region as determined by Tukey's HSD analyses 63

Table 4-1. Collection sites for nestling Burrowing Owl feather samples.............98

Table 4-2. The isotopic delineation of Burrowing Owl collection areas across study region as determined by Tukey's HSD analyses 100

Table 4-3. Long distant migrants as determined by stable-isotope tracking.....103

Table 4-4. Feather types collected from wintering Burrowing Owls................104

List of Figures

Figure 2-1. The relationship between experimental groups of quail and falcons...32

Figure 2-2. A comparison between a potential change in δD values of the precipitation and the initial δD values of multiple groups of quail 33

Figure 2-3. The effects of a diet switch on δD values in Japanese Quail feathers..34

Figure 2-4. The effects of a diet switch on δD values in Peregrine Falcons feathers 35

Figure 3-1. Feather collection regions of natal Peregrine Falcons as determined by GLM analyses and post-hoc Tukey's HSD tests 66

Figure 3-2. The relationship between δD_n and $\delta^{13}C$ values of natal Peregrine Falcon feathers collected across northern North America 67

Figure 3-3. Frequency distribution of migrant falcons categorized into regional alpha-codes 68

Figure 3-4. Plots of 67 migrant feathers with origins determined by the relationship between δD_n and $\delta^{13}C$ values 69

Figure 4-1. Feather collection regions of natal Burrowing Owls as determined by GLM analyses and post-hoc Tukey's HSD tests 105

Figure 4-2. The relationship between δD_n values of Burrowing Owl feathers and the latitude of the collection sites 106

Figure 5-7. The relationship between the number of fledglings produced per pair of Burrowing Owls and the relative size of the breeding population in the subsequent year as predicted by $NY_{+1} = N_R - \Delta E$..**164**

Figure 6-1. A comparison of isotope values of similar locations in the Peregrine Falcon and Burrowing Owl reference datasets............................**187**

Chapter 1

Introductory chapter

The study of animal migration leads to a better understanding of the connectivity between a species and its ecological requirements in different regions. Whether or not populations migrate *en masse* to the same wintering location or if they disperse across large areas has consequences for conservation and management of the species and its habitats (Webster et al. 2002). To understand migration patterns is important since animals spend significant amounts of time in geographically and potentially ecologically different areas. Successes and failures during the breeding season can have a direct affect on the successes and failures of the wintering season, and vice versa (Webster et al. 2002). Nesting success and recruitment may be predetermined by the quality of the wintering habitat. Survival over winter may depend on the preparedness of the animal at the end of a summer. The connection between the summer and winter events are complicated with requirement to survive migrations. If conservation and management efforts are to be successful, the population dynamics during a complete annual cycle must be understood.

Under Priority 1 of the *Anatum* Peregrine Falcon Recovery Plan, the origins of toxic DDT metabolites found in the falcons' tissues were to be identified (Erickson et al. 1988). Sources unrelated to their breeding grounds could only be located with the knowledge of where Peregrine Falcons (*Falco peregrinus*) migrated and wintered. Band recoveries have demonstrated the incredible migratory range of the falcons. Peregrines banded in North America have been recovered all over the Western Hemisphere as far south as Argentina (Erickson et al. 1988, Yates et al. 1988). Of two falcons banded on the same breeding grounds in the central Arctic, one wintered in California and the other in central Chile (Erickson et al. 1988). Band recoveries established links between the breeding populations of North America and possible sources of contaminants in the winter. Captures of Peregrines at migration monitoring stations helped establish migratory routes (Yates et al. 1988). Recently, satellite tracking has provided detailed information about the daily flight distances, stopover sites and speeds travelled by the falcons (Fuller et al. 1998, Holroyd and Duxbury 1999). Leg bands and satellite transmitters have been important tools for Peregrine Falcon conservation in the western hemisphere.

The migration routes and wintering locations of Burrowing Owls (*Athene cunicularia hypugaea*) breeding in western North America are not as well documented as those of Peregrine Falcons. A North American Conservation Action Plan, a product of the Second Annual Burrowing Owl Symposium in Ogden, Utah in 1998, called for research on migration routes and wintering grounds (Holroyd et al. 2001). Satellite transmitters are currently too large for use on the small owls, thus to date, what has been determined has been derived from band recoveries and radio-telemetry. Band returns have shown that populations north of southern California and southern Arizona are migratory (Haug et al. 1993). Fall recoveries of Canadian bred owls indicated a southwestern direction towards Texas and Mexico (Haug et al. 1993). However, the winter range of owls that breed in Canada has been unknown until recently. During the winter of 1998, a banded Burrowing Owl from Saskatchewan was recovered in southern Texas. In 2001, owls carrying radio transmitters from Alberta and Saskatchewan were relocated near Galveston and McAllen, Texas; northern Veracruz State, Mexico; and Michoacan State, Mexico (G. Holroyd unpubl. data). The mid-summer, southern Saskatchewan recapture of an owl banded in the spring of 2003 in southern Arizona is perhaps the most important band recovery to date for the species (C. Conway unpubl. data). The recapture was remarkable because the female owl was banded as a breeding adult at a burrow that failed. The owl subsequently traveled over 2000 km in the same breeding season to raise a brood of seven owls in southern Saskatchewan (G. Holroyd unpubl. data). These important links between Canadian populations, migration routes and wintering grounds were made with the use of banding and telemetry.

Mark and recapture systems have been effective in providing general information about Peregrine Falcons and Burrowing Owls, but the information has taken many years to accumulate. From 1927 to 1990, only 27 bands were recovered from banded Burrowing Owls during winter months (Haug et al. 1993). Of all bands put on Burrowing Owls from 1955 to 2002, only 272 of 19,027 (1.4%) have been recovered (USGS 2003). While Peregrine Falcon band recoveries have been more numerous, the probability of a recovery has not been high. Of 36,836 Peregrines banded between 1955-2002, only 2779 (7.5%) were recovered (USGS 2003). In fact, the standard methods of bird-banding produces very low recovery rates for most non-game species, and radio/satellite tracking at a continental scale are associated with a requirement of substantial resources (Hobson 2002). The previous frustrations of low recovery rates associated with standard migration tracking techniques are being alleviated by new or improved techniques such as stable-isotope analysis (Hobson 2002, Webster et al. 2002).

Stable-isotope analysis (SIA) was a product of the University of Chicago during the 1930's and 1940's (Urey et al. 1932, Urey 1947). Names such as Urey, Epstein, McKinney, McCrea and Neir are synonymous with the original development of the theory and instrumentation for analyzing inorganic and organic material for their isotopic ratios. SIA was originally used by geochemists to examine processes such as isotope hydrology, geomorphological pathways and palaeoclimatology (Schiegal 1972, Kharaka and Carothers 1980, Muehlenbachs 1986, Sheppard 1986, Ehleringer and Rundel 1989, Sternberg 1989). Geochemists were also the first to realize that stable-isotope ratios changed in biological systems and began to determine how and why the ratios changed (Wickman 1952, Craig 1953, Park and Epstein 1960). Naturally occurring stable-isotopes are found in the elements most important to biological processes: carbon, nitrogen, hydrogen, oxygen, sulphur and phosphorus. The development of SIA helped determine the relative amount of isotopes in organic and inorganic matter, how these ratios are altered and finally, how they could be used in the investigation of natural systems. Because stable-isotopes do not decay, they can be used to investigate biological processes since their ratios can be traced through natural systems using mass spectrometry (Peterson and Fry 1987, Ehleringer and Rundel 1989, Lajtha and Michener 1994).

The usefulness of stable-isotope ratios stems from a process called fractionation. The key property of isotopes that leads to fractionation is a difference in mass between the isotopes of a given element (Peterson and Fry 1987, Schimel 1993). Within the nucleus of the atom, isotopes of the same element have the same number of protons, but differ in the number of neutrons. The atoms with more neutrons have a greater mass (heavy isotopes). In reference to stable-isotope dynamics, fractionation is a change in the amount of heavy isotopes relative to light isotopes in the product of a physical or chemical reaction. Because lighter isotopes have relatively less mass, they have higher velocities during reactions and can subsequently react at a faster rate. Heavier isotopes form stronger bonds in molecules and are less reactive (Schimel 1993). Therefore, during a reaction or process that causes fractionation, lighter isotopes are consumed at a faster rate in the formation of new products. Over time, concentrations of heavier isotopes are altered between reactants and products.

SIA provides a relatively new method to trace migratory animals back to their nutritional, natal or breeding grounds without having been previously banded (Hobson 1999a). Hydrogen isotope ratios (δD) in precipitation can be altered by changes in temperature, distance from maritime systems and changes in altitude (Dansgaard 1964, Kharaka and Carothers 1980, Sheppard 1986). These ratios exist in predictable patterns across North America and Chamberlain et al. (1997) and Hobson and Wassenaar (1997) were first to demonstrate that the hydrogen isotope ratios are passed up food chains to create similar continental patterns in the feathers of birds. The average carbon isotope ratios (δ^{13}C) of ecosystems can differ based on the dominant type of photosynthesis (C3, C4, CAM) of plants or differences in enzymatic reactions and water use efficiency at varying levels of relative humidity (Körner et al. 1991, Lajtha and Marshall 1994, Hobson and Wassenaar 2001, Graves et al. 2002, Rubenstein et al. 2002). Nitrogen isotope ratios (δ^{15}N) in food webs are fractionated by various nitrogen fixing processes of plants. The resulting isotope ratios are also dependent upon soils that have variable nitrogen dynamics (Shearer et al. 1978, Schulze et al. 1994, Michelsen et al. 1996, Graves et al. 2002). Anthropogenic enrichment associated with agriculture can also create differences in nitrogen isotope ratios in plants and animals (Duxbury 1998, Hebert and Wassenaar 2001). Ratios of carbon and nitrogen stable-isotopes are also fractionated depending upon how many trophic levels exist below the study species in a food-web system (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1992, Hobson 1993). The above-mentioned causes of fractionation produce large-scale, continental patterns that can be ultimately detected in animal tissues through SIA (Hobson 2002).

Over the past two decades, stable-isotopes have been used to investigate the nutritional, natal or breeding origins of migratory animals. Hobson (1999a) lists 34 studies that examined the movements of terrestrial and aquatic mammals, birds, fish and arthropods. Similar studies have continued and SIA has been used recently to examine the migration of songbirds (Hobson 1999b, Chamberlain et al. 2000, Wassenaar and Hobson 2000, Hobson and Wassenaar 2001, Hobson et al. 2001, Wassenaar and Hobson 2001, Kelly et al. 2002, Rubenstein et al. 2002), raptors (Meehan et al. 2001, Lott et al. 2003), waterfowl (Caccamise et al. 2000, Hobson et al. 2000, Hebert and Wassenaar 2001), seabirds (Cherel et al. 2000), seals (Burton and Koch 1999), fish (Kline et al. 1998, Doucett et al. 1999, Åkesson 2002), and shrimp (Fry et al. 1999).

This dissertation presents the results of the application of SIA to answer questions about the migratory and dispersal movements of Peregrine Falcons and Burrowing Owls. SIA was applied to feathers collected from birds on their breeding grounds, from birds on migration, or from birds on their wintering grounds. Feathers provided samples of inert protein (keratin) that could be collected without harm to the birds and easily stored.

The second chapter is an examination of what type of feather should be used to create isotope reference datasets or base-maps. In the case of Peregrine Falcons, the timing of nest visits may correspond with various nestling plumage stages. Since the falcons are known to use endogenous nutrients in the formation of eggs, it is assumed that natal down would carry the isotopic signature of the migratory adult female. The question investigated is at what plumage stage does a feather reflect the local food source thereby providing accurate isotope values for the creation of a reference dataset or base-map? A diet switch experiment with Japanese Quail and captive bred Peregrine Falcons is used to determine what plumage stage should be sampled for isotope analysis.

In chapter three, SIA is used to determine the summer origins of Peregrine Falcons captured at a migratory concentration point during their fall migration. Years of band recoveries have indicated where and when the falcons migrated, but the rarity of band recoveries has always meant this was a prolonged process. With the use of SIA, each falcon trapped on migration can be traced back to its natal origin without the dependence on leg bands. SIA combined with information gathered when the migrating falcons are trapped provides additional information that can be used to monitor falcon populations. Since Arctic populations are very expensive to survey, SIA is demonstrated as a more practical method of remotely monitoring these northerly populations.

In the fourth chapter SIA is used to answer questions about the migratory patterns of the Burrowing Owl. Recently, some wintering locations of Burrowing Owls that bred or hatched in Canada were discovered. These winter locations contain many other owls that are not banded. SIA is used to investigate the proportion of owls in the winter locations that may be from breeding populations in Canada relative to other populations across western North America.

The focus of the fifth chapter is on the northern populations of Burrowing Owls. SIA is used to examine inter-year movements of the owls between populations in the northern Great Plains. One of the key aspects of population modelling is adult survivorship. To obtain accurate estimates of survivorship, rates of emigration must also be determined. Philopatric band recoveries are uncommon, but inter-population band recoveries are even more rare. With SIA, after-hatch-year owls that arrive from their wintering grounds are compared to the isotopic signature of owl populations in the area. Large-scale inter-population dynamics of Burrowing Owls were examined. Specifically, the net movement of owls into and out of populations is investigated.

The concluding chapter provides a synopsis of the findings of each of the main chapters of this dissertation. With the results of the SIA applications established in the preceding chapters, the practicality of SIA as a tool for monitoring populations and migrations is compared with methods that are more traditional. Finally, suggestions for future research are presented.

Literature Cited

Åkesson, S. 2002. Tracking fish movements in the ocean. Trends in Ecology and Evolution17:56-57.

Burton, R.K and P.L. Koch. 1999. Isotopic tracking of foraging and long-distance migration in northeastern Pacific pinnipeds. Oecologia 119:578-585.

Caccamise, D.F., L.M. Reed, P.M. Castelli, S. Wainwright, T.C. Nichols. 2000. Distinguishing migratory and resident Canada Geese using stable-isotope analysis. Journal of Wildlife Management 64:1084-1091.

Chamberlain, C.P., S. Bensch, X. Feng, S. Åkesson and T. Andersson. 2000. Stable-isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. Proceedings of the Royal Society of London 267:43-48.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecolgia 109:132-141.

Cherel, Y., K.A. Hobson and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155-162.

Craig, H. 1953. The geochemistry of stable carbon isotopes. Geochimica Cosmochimica Acta 3:53-92.

Dansgaard, W. 1964. Stable-isotopes in precipitation. Tellus 16:436-468.

Doucett, R.R., R.K. Booth, G. Power and R.S. McKinley. 1999. Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights from stable-isotope analsyis. Canadian Journal of Fisheries and Aquatic Science 56:2172-2180.

Duxbury, J.M. 1998. An application of stable-isotope ecology to the study of raptor diets. MSc thesis, University of Alberta, Edmonton, Alberta, Canada. 150 pp.

Ehleringer, J.R. and P.[illegible] Rundel. 1989. Stable isotopes: history, units, and instrumentation. Pages 1-15. *In* Stable Isotopes in Ecological Research. Ecological Studies V. 68. P.W. Rundel, J.R. Ehleringer and K.A Nagy [Eds.], Springer-Verlag New York Inc., New York.

Erickson, G. L., R. Fyfe, R. Bromley, G. Holroyd, D. Mossop, B. Munro, R. Nero, C. Shank, and T. Weins. 1988. Anatum Peregrine Falcon recovery plan. Canadian Wildlife Service, Ottawa, ON. 52 pp.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic composition. Limnology and Oceanography 33:1182-1190.

Fry, B., P.L. Mumford and M.B.Robblee. 1999. Stable isotope studies of Pink Shrimp (*Farfantepenaeus duorarum* bukenroad) migrations on the southwestern Florida shelf. Bulletin of Marine Science 65:419-430.

Fuller, M.R., W.S. Seegar and L.S. Schueck. 1998. Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the western hemisphere. Journal of Avian Biology 29:433-440.

Graves, G.R., C.S. Romanek, and A.R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proceedings of the National Academy of Science 99: 8096–8100.

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl (*Speotyto cunicularia*). *In:* A. Poole and F. Gill (eds.), The Birds of North America, No. 61. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hebert, C.E. and L.I. Wassenaar. 2001. Stable Nitrogen Isotopes in Waterfowl Feathers Reflect Agricultural Land Use in Western Canada. Environmental Science & Technology 35: 3482-3487.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue dependent stable-isotope models. Marine Ecology Progress Series 95:7-18.

Hobson, K.A. 1999a. Tracing origins and migration of wildlife using stable-isotopes: a review. Oecologia 120:314-326.

Hobson, K.A. 1999b. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. Condor 101:799-805.

Hobson, K.A. 2002. Science's Compass: Incredible journeys. Science 295:981-982.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using 13C and 15N analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K.A. and L.I. Wassenaar . 1997. Linking breeding and wintering grounds of neotropical migration songbirds using stable isotopic analysis of feathers. Oecologia 109:142-148.

Hobson, K.A., R.B. Brua, W.L. Hohman, L.I. Wassenaar. 2000. Low frequency of "double molt" of remiges in Ruddy Ducks revealed by stable-isotope: Implications for tracking migratory waterfowl. Auk 117:129-135.

Hobson, K.A. and L.I. Wassenaar. 2001. Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. Ecological Applications 11:1545-1553.

Hobson, K.A., K.P. McFarland, L.I. Wassenaar, C.C. Rimmer, and J.E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable-isotope analyses of feathers. Auk 118:16-23.

Holroyd, G.L., R. Rodríguez-Estrella and S.R. Sheffield. 2001. Conservation of the Burrowing Owls in western North America: issues, challenges and recommendations. Journal of Raptor Research 35:399-407.

Holroyd, G.L. and J.M. Duxbury. 1999. Travels of Peregrine Falcon #5735. Blue Jay 57: 146-149.

Kelly, J.F., V. Atudorei, Z.D. Sharp and D.M Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216-221.

Kharaka, Y.K and Carothers, W.W. 1980. Oxygen and hydrogen isotope geochemistry of deep basin brines. Pages 305-360. *In* Handbook of Environmental Isotope Geochemistry, *Edited by* P. Fritz and J.CH. Fontes, Amsterdam.

Kline, T.C. Jr., W.J. Wilson and J.J. Goering. 1998. Natural isotope indicators of fish migration at Prudhoe Bay, Alaska. Canadian Journal of Fisheries and Aquatic Science 55:1494-1502.

Körner, C., F.D. Farquhar, and S.C.Wong. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia 88:30-40

Lajtha, K. and J.D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. Pages 1-21 *in* K. Lajtha and R.H. Michener [Eds.], Stable-isotopes in ecology and environmental science. Blackwell, Oxford

Lajtha, K. and R.H. Michener [Eds.]. 1994. Stable Isotopes in Ecology and Environmental Science. Blackwell, Oxford

Lott, C.A., T.D. Meehan and J.A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulphur isotopes in feathers: influence of marine prey base. Oecologia 134:505-510.

Meehan, T.D., C.A. Lott, Z.D. Sharp, R.B. Smith, R.N. Rosenfield, A.C. Stewart, and R.K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. Condor 103:11-20.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53-63.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochemica Cosmochemica Acta 48:1135-1140.

Muehlenbachs, K. 1986. Alteration of the oceanic crust and the 18O history of seawater. Pages 425- 445 *In* Stable Isotopes in High Temperature Geological Processes. *Edited by* J.W.Valley, H.P. Taylor, Jr. and J.R. O'Neil. Mineralogical Society of America - BookCrafters, Inc., Chelsea, Michigan.

Park, R. and S. Epstein. 1960. Carbon isotope fractionation in plants. Geochimica Cosmochimica Acta 21:110-126.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Rubenstein, D.R., C.P. Chamberlain, R.T. Holmes, M.P. Ayres, J.R. Waldbauer, G.R. Graves and N.C.Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. Science 295:1062-1065

Schiegal, W.E. 1972. Deuterium content of peat as a paleoclimatic recorder. Science 175:512-513.

Schimel, D.S. 1993. Distribution and fractionation of isotopes in the environment. Pages 35-113 *In* Theory and Application of Tracers. *Edited by* E.A. Paul and J.M. Melillo, Academic Press, Toronto.

Schulze, E.D., F.S. Chapin, III and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406-412.

Shearer, G., D.H. Kohl, and S.-H. Chien. 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America Journal 42:899-902.

Sheppard, M.F. 1986. Characterization and isotopic variations in natural waters. Pages 165-183 *In* Stable Isotopes in High Temperature Geological Processes. *Edited by* J.W.Valley, H.P. Taylor, Jr. and J.R. O'Neil. Mineralogical Society of America - BookCrafters, Inc., Chelsea, Michigan.

Sternberg, L. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. Pages 124-141 *In* Stable Isotopes in Ecological Research. Ecological Studies V. 68. P.W. Rundel, J.R. Ehleringer and K.A. Nagy [Eds.], Springer-Verlag New York Inc., New York.

Urey, H.C. 1947. The thermodynamic properties of isotopic substances. Journal of the Chemical Society (London) 1947:562-581.

Urey H.C., F.G. Brickwedde, and G.M. Murphy. 1932. A hydrogen isotope of mass 2. Physical Review 39:164-165.

USGS. (United States Geological Survey). 2003. Non-Game Banding Records 1955 – 2002. http://www.pwrc.usgs.gov/pubdata/pubdata.htm.

Wassenaar L.I. and K.A. Hobson. 2000. Evaluating the use of stable-carbon (δ^{13}C) and H (δD) isotope ratios in feathers to infer breeding origins of Red-winged Blackbirds. Ecological Applications 10:911-916.

Wassenaar, L.I. and K.A. Hobson 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. Environmental Science and Technology 35:1845-1850.

Webster, S.M, P.P Marra, S.M. Haig, S. Bensch and R.T. Holmes. 2002. Links between worlds: unravelling migratory connectivity. Trends in Ecology and Evolution 17:76-82.

Wickman, F.E. 1952. Variations in the relative abundance of the carbon isotopes in plants. Geochimica Cosmochimica Acta 2: 636-639.

Yates, M.A., K.E. Riddle and F.P. Ward. 1988. Recoveries of Peregrine Falcons migrating through the eastern and central United States, 1955-1985. Pages 471-483 *In* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], Peregrine Falcon populations: their management and recovery. The Peregrine Fund Inc., Boise, ID.

Chapter 2

Changes in hydrogen isotope ratios in sequential plumage stages[2]

The analysis of stable-isotopes for the study of the migration and movements of a wide variety of animals is becoming more common [1-12]. Naturally occurring, continental gradients of stable-isotope ratios have been very useful to estimate the summer origin of wintering populations [6 -12]. The approximate origin of migrating and wintering birds has been delineated with the use of the naturally occurring ratios of isotopes based on the principle that the isotopes in the tissues reflect the diet of the bird during the growth of the tissue [1,13,14,15].

Continental patterns in the stable-isotope ratios of hydrogen (δD) have been the key for estimating the origin of migratory animals [1,5-12,16]. To date, most studies that have used δD to delineate the origin of migrating and wintering birds have relied on stable-isotope patterns linked to continental precipitation cycles [5-7, 10-12]. However, bird movements interpolated solely from isotope patterns in precipitation may been over- or underestimated. For example, the continental pattern of hydrogen isotopes in precipitation was used to locate the origin of wintering Worm-eating Warblers (*Helmitheros vermivorus*) but some of the warblers apparently originated in central Ontario, about 600 km north of their known range [11]. A more precise method for retracing the origin of migratory animals evolved when isotope base-maps were based on tissues where the exact location of their growth was known [5,6,8,9]. The analysis of feathers collected at nest sites from nestlings or juveniles provides a more precise measure of the local δD [6]. The establishment of a link between migrant feathers and natal feathers collected at the nest would likely be more reliable than an association between feathers and isotope ratios of precipitation. Taken further, the isotope values from nestlings' feathers used in conjunction with values from documented background isotope patterns will likely increase the level of accuracy with which migrants can be tracked [5,6].

---

[2] *A version of this chapter was published as Duxbury, J. M., G.L. Holroyd and K. Muehlenbachs. 2003. Changes in hydrogen isotope ratios in sequential plumage stages: An implication for the creation of isotope-base maps for tracking migratory birds.* Isotopes in Environmental and Health Studies *39(3): 179-189.*

When the young of precocial bird species hatch, they are immediately mobile and may only be briefly available for sampling before they leave the nest, making them relatively inaccessible. Precocial species hatch while in the process of growing a substantial set of natal down feathers and usually do not develop their juvenile plumage until after leaving the nest [17]. Altricial nestlings hatch in a helpless condition that requires parental care for some time [17]. During the time required for maturation at the nest site, the hatchlings will grow feathers in three stages. Usually, the hatchlings are covered in a fine natal down when they escape from their shells. A second, more substantial, juvenile down overgrows the fine down. Finally, the nestling begins to grow its juvenile plumage, which consists of complete body and flight feathers [17]. In small passerine species, this process takes place over 2-3 weeks. However, in larger species such as Peregrine Falcons (*Falco peregrinus anatum*), this process can take over a month [18, 19].

Since hatchlings are born with some natal down feathers, the nutrients that were used to form those feathers must be derived from maternal sources [17,20]. Therefore, the isotope ratios in natal down will reflect those of the females. Whether or not the maternal isotope ratios are indicative of the isotope signatures of local prey or that of prey eaten during the winter or spring migration, will depend on isotope ratio turnover rates, whether the formation of eggs began before or after the ingestion of prey local to the breeding area (income vs. capital breeding [21]), and the mobilization of stored tissue to form the eggs. Dependence on endogenous nutrients in the formation of eggs in waterfowl may be related to the latitude at which they breed [22]. Temperate-breeding waterfowl species have access to food on arrival at their breeding grounds. Unlike Arctic-breeding species, temperate breeders do not depend on endogenous reserves to initiate their reproductive systems [21,22,23]. For example, female Redhead Ducks can produce eggs without mobilizing endogenous resources [22]. Given that Peregrine Falcon eggs contain levels of DDT metabolites that are correlated with levels in the blood of maternal females exposed to DDT in winter [24], the falcons must utilize some endogenous nutrients in the eggs that had been obtained in other regions of their migratory cycle.

A reproductive bird may only have to be on a specific diet for a week before forming eggs that would be reflective of the carbon isotopic signal of its food [25]. The δD in flight feathers of Japanese Quail (*Coturnix japonica*) can reflect diet manipulations prior to the growth of those feathers [22,26]. However, to what degree diet manipulation can be detected in the juvenile down feathers of quail is not known. Specifically, the amount of change in δD values from egg formation through multiple plumage stages has not been determined.

Peregrine Falcons have relatively long nestling periods (~40 days). The timing of the replacement of δD values associated with imported endogenous nutrients with δD values of exogenous nutrients from local prey determines the best plumage to sample for the creation of an accurate isotope reference dataset for the falcons. The maternal isotopic signature should not contribute towards what is considered to be the local stable-isotope signal. Since many Peregrine Falcon nests are not easily accessible, knowledge of which plumage stage reflects the isotopes of locally obtained nutrients would help determine when to visit nests to collect samples for isotope analyses.

Laboratory experiments can provide initial direction and/or background information for field studies that utilize stable-isotope analysis (27-29). To determine what plumage stage isotopically reflects a new dietary source, and therefore the optimal timing of field nest visits for sampling, a diet manipulation experiment was conducted with the use of captive Japanese Quail and captive bred Peregrine Falcons.

Methods

This experiment was conducted at the Upsan Downs Peregrine Falcon breeding facility 50 km east of Edmonton, Alberta between April and May, 2002. The food and drinking water of newly hatched Japanese Quail and Peregrine Falcons was changed and changes in δD values through sequential plumage stages were monitored. Maternal endogenous nutrients with a given isotope signature were replaced with exogenous nutrients during the growth of different plumages.

Two isotopically different batches of quail feed were sought for manipulating the diet in the quail experiment. While the sources of the feed were separated geographically, the δD of the feed were only marginally different (Table 2-1). The contribution of hydrogen molecules of drinking water to the formation of organically bound hydrogen in animal tissue has been debated [30-32]. However, it has been demonstrated that significant differences in δD values in drinking water can lead to significantly different δD values in feather tissues [22,26]. Therefore, two isotopically distinct sources of water were used to supplement the diets in order to create a larger disparity between the control and treatment diets (Table 2-1). The quail and falcons were provided with free access to drinking/bathing water that was drawn from large capacity storage containers in which fractionation due to evaporation was kept to a minimum.

Quail

At the falcon breeding facility, quail are raised without mixing hatches, and each hatch is provided with identical rearing conditions. Five weeks preceding this experiment, pens of breeding quail were switched to D-enriched food and water in order to produce enough food for the treatment group of falcon young (Figure 2-1). Hatchlings of the D-enriched quail were maintained on the same diet and water and served as the control group for the quail study. Quail selected for the treatment group were immediately provided with feed and water that were relatively more negative than those provided to the control group. Ten newly hatched quail were randomly chosen from each of three batches of control and treatment quail for a total of 30 in the control group and 30 in the treatment group (Figure 2-1).

Natal down feathers were sampled from the young quail less than 24 hours after they hatched. Each quail was marked to identify it for subsequent sampling. After one week, the juvenile plumage was present, but feather growth was insufficient to provide an adequate sample. Consequently, complete juvenile feathers were sampled when quail chicks were two-weeks old.

Falcons

All breeding falcons were provided with the same food and water throughout the egg laying and incubation periods. Thus, the control and treatment nestlings theoretically began with comparable values in their natal down, plumage derived from maternally endogenous nutrients in the eggs [17,20,25].

Thirteen juveniles were used in the Peregrine Falcon study. Falcon nestlings from a single brood were kept together and fed the same diet and water. Two broods of three young each were used as the control group, and three broods of two or three nestlings formed the treatment group (Figure 2-1).

The young Peregrine Falcons were hand-fed quail breast meat from hatch to five days of age. At the falcon breeding facility, meat that is to be fed to newly hatched falcons is soaked in water to aid consumption. To maximize the D-isotopic difference between the experimental falcon diets, the quail breast meat was soaked in either D-enriched or D-depleted water corresponding to the treatment or control groups. After five days of age, adult falcons in their nesting chambers fed the young. The treatment group that was provided with the D-enriched diet simulated the situation where reproductive females arrive at their breeding site with endogenous reserves that differ in δD to the local prey. Nestling feathers were sampled at the natal down, juvenile down and juvenile plumages over one month.

Hydrogen atoms of organic tissues that are exchangeable with ambient water vapour have led to an analytical issue because changes in the total δD of tissues can be attributed to changes in the δD of the water vapour along with changes in experimental treatments [10,26,33,34]. To minimize potential exchange effects, the samples were grown, sealed *en vacuo* and analyzed locally without delay. With the feather samples sealed in evacuated quartz tubing, the feathers' exchangeable hydrogen could not be altered by the laboratory ambient water vapour. But the problem of exchangeable hydrogen was not completely solved. Since the fractionation of D/H ratios is temperature dependent, differences in δD in precipitation can potentially vary in the order of 30‰ between seasons at a single locale [35]. Alterations in the δD of the ambient water vapour associated with changes in local precipitation during the course of the experiment could lead to erroneous results. However, a limitation in the design of the quail experiment provided a check to determine if and by what magnitude the data may have drifted due to hydrogen exchange with ambient water vapour. Due to the capacity of the quail rearing operation, one batch of eggs was hatched at a time. This drawback introduces a temporal bias to the study design, but it also provides the opportunity to determine if there is a significant drift in the data that could be due to time exposed to potentially changing δD values in the local water vapour. The only variable that was different for newly hatched quail was the day they hatched. Therefore, the mean change between subsequent batches of quail was compared to the mean change in δD values between mid May and Mid June. Five years of δD values in precipitation measured from 1961-1965 in Edmonton were available for an evaluation [35]. The mean change from mid May to mid June was used in the comparison with changes between the batches of quail, as this was the same time the experiment was conducted.

Since the batches of quail were produced and sampled one at a time, a temporal bias was introduced. The samples therefore lacked independence and inferential statistics would be invalid due to pseudoreplication [36]. The conditions and timing of treatments for the falcons was identical, ensuring the independence between the groups of falcon young required for the application of inferential statistics [36].

All feather samples were cleaned with a 2:1 chloroform-methanol solution to remove surface oils and any remnant lipids. The samples, along with cupric-oxide, were then sealed under vacuum in quartz tubing in preparation for combustion for off-line analysis [10, 11]. Water vapour generated by the combustion process was cryogenically isolated and reduced to hydrogen over hot zinc [37]. The resultant hydrogen was analyzed using a duel-inlet, Finnigan-MAT 252 mass spectrometer. δD values are reported in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. Results were normalized using VSMOW/GISP/SLAP scale. Sample reproducibility during this experiment was determined to be better than ± 2.0‰.

Results

Quails

The difference between the control and treatment water was much greater than in the feed (32‰ vs. 3‰ respectively, Table 2-1). Repeated measures (*n*=5) of the water during the experiment led to standard deviations of 1.75‰ (control) and 0.79 ‰ (treatment). The feathers collected for both the treatment and control groups had grown to equal lengths (Table 2-2).

The mean change in *δ*D values of precipitation between mid May and mid June in the Edmonton region over a five-year period was a positive shift from –125.94‰ (± 1 SD = 33.9‰) to –106.16‰ (± 1 SD = 17.0‰)(Figure 2-2). If a large shift in the *δ*D value of the ambient water vapour took place during the experiment, it did not appear to cause a drift in the data. Measurements of consecutive batches of quail indicate either a small negative drift, or no drift at all (Figure 2-2). Therefore, it was assumed that hydrogen exchange between ambient water vapour and the feather samples was kept to a minimum.

The *δ*D values for the quail in the three control groups did not significantly change over the duration of the experiment (Table 2-3, Figure 2-3). *δ*D values for the treatment groups were more D-depleted by an average of 20‰ over the same two-week time period (Table 2-3, Figure 2-3).

Falcons

The control and treatment diets did not produce measurable differences in the length of body feathers during development (*t*-test, $t = -1.11$ p=0.272, Table 2-2). The Peregrine Falcon nestling feathers in the control groups had consistent mean *δ*D values throughout the duration of the experiment (Table 2-4, Figure 2-

4). The mean changes from the natal down to the juvenile down feathers, and from juvenile down to the juvenile plumage were within the analytical error of the mass spectrometer (± 2.0‰). The lack of detectable changes in δD values indicated no significant change between plumage stages where the falcon nestlings were provided with an isotopically consistent diet.

The mean δD values in the feathers of the falcons in the treatment group increased from the beginning to the end of the experiment (Table 2-4, Figure 2-4). A D-enrichment in the relative amount of deuterium of 19‰ from natal down to juvenile down was highly significant (paired *t*-test, $t = -17.15$, $p < 0.0001$). The increase continued as the juvenile body feathers were found to be moderately enriched another 3‰ relative to the juvenile down feathers (paired *t*-test, $t = -2.18$, $p = 0.072$).

Discussion

The incorporation of isotopic signatures of endogenous resources into early plumage stages depends on the relative amount of maternal nutrients used in the formation of eggs and their contents. The objectives of these experiments were to determine at what plumage stage were hydrogen isotope ratios reflective of a switch in food sources in a precocial and an altricial species. The plumage stage that best reflected an experimental diet switch would theoretically mirror the switch from endogenous winter nutrients to local food resources for wild birds.

The plumage stage that best represents the local isotopic signature would be the ideal to collect for the purpose of creating an isotope base-map or dataset.

The captive quail had unlimited access to food and water during follicle development and could have theoretically created eggs utilizing only exogenous resources. Similar to other experiments using captive quail [25], the δD values of feathers from young quail in this study suggest that unlimited food may not deter the input of some endogenous resources into eggs. Therefore, creating δD base-maps or reference datasets for migratory precocial species, even if they have access to food resources, may prove unreliable.

Since some Peregrine Falcon eggs in the wild contain chemicals only found on the falcons' wintering grounds [38], endogenous reserves must be utilized in the production of their eggs. The juvenile plumage of the falcons is not well developed until the fourth and fifth week after hatch. Four weeks appears to be enough time for the feathers of nestlings to reflect the δD values of their local diet. While the second down of the falcons was found to be significantly different than the natal down, it was only moderately different from the body feathers; thus second down could also be used for the creation of an isotope base-map or reference dataset though body feathers are recommended. The potential use of the second plumage stage for isotope geo-referencing is important since nesting attempts are not initiated at the same time. Some nests visits may occur when the body feathers are not large enough to be sampled. In such a case, a sample of the second down should be taken just in case a return visit is not possible. The resulting analysis will provide a good estimate of the isotopes ingested by the nestling. If only single trips to nests are possible, visits should take place approximately 4 weeks after the presumed hatch of the falcons.

While this study measured changes in δD values at defined intervals, it did not include analyses of muscle and lipid tissue and blood of predator and prey that is required to develop an exponential model necessary to determine the turnover rate [27,28,37,39]. To determine the relative proportion of exogenous and endogenous nutrients that actually go into the creation of eggs, embryos and developed tissues of Peregrine Falcons, a multiple-source mixing-model should be conducted [22,37]. Such base-line information would be of use for studying migrant Peregrine Falcons, as well as other migratory birds, since δD values in nestlings could be used to approximate the migratory and arrival schedules of adults.

Acknowledgements

Thanks go to P. and H. Trefry for access to the falcons and quail that were used for this experiment, and P. Trefry and L. Priestley for their assistance in conducting the experiment. The Natural Science and Engineering Council of Canada (NSERC) and Environment Canada provided funding for this study.

Table 2-1. Results from hydrogen isotope analyses of feed and water used in the diet switch experiment involving Japanese Quail. Results listed in δD‰. The deuterium depleted control water came from the Edmonton municipal water supply, which originates from rainfall and glaciers in the mountains west of the study location. The treatment water came from rainfall collected in water barrels at the Upsan Downs farm, 40km east of Edmonton, Alberta.

	Feed Mean ± 1 SD	**Water Mean ± 1 SD**
Control Diet (*n*=5)	-113 ± 2	-110± 2
Treatment Diet (*n*=5)	-116± 1	-143± 1
Difference	3	32

Table 2-2. Feather length comparisons between control and treatment groups of Peregrine Falcons and Japanese Quail.

Group	**Feather Length (mean ± 1 SD mm)**		
	Natal Down	**Juvenile Down**	**Juvenile Plumage**
Quail			
Control	5.32 ± 0.24	n/a*	16.29 ± 0.64
Treatment	5.27 ± 0.22	n/a*	16.45 ± 0.62
Falcons			
Control	n/a[1]	n/a[1]	23.73 ± 1.49
Treatment	n/a[1]	n/a[1]	23.73 ± 2.07

* Japanese Quail do not have this plumage stage

[1] Not measured

Table 2-3. Hydrogen isotope analyses of Japanese Quail feathers. Results listed in δD ‰.

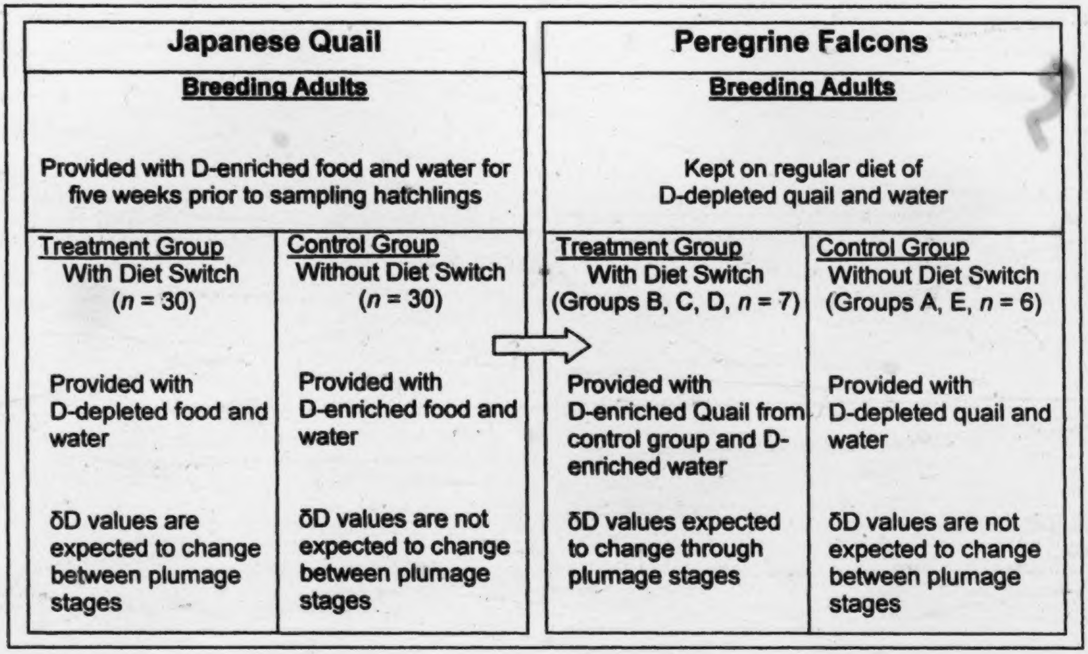
	Time 1 (Start)	Time 2 (After 2 weeks)	
	Mean ± 1 SD	Mean ± 1 SD	Change
Control Group			
C1 (*n* = 10)	-113± 2	-112± 2	+1
C2 (*n* = 10)	-115± 2	-115 ± 2	0
C3 (*n* = 10)	-121± 1	-121± 2	0
Whole Group (*n* = 30)	-116± 4	-116 ± 5	0
Treatment Group			
E1 (*n* = 10)	-111 ± 2	-134 ± 1	-23
E2 (*n* = 10)	-116 ± 2	-133 ± 2	-17
E3 (*n* = 10)	-115 ± 2	-133 ± 2	-18
Whole Group (*n* = 30)	-114 ± 3	-133 ± 2	-19

Table 2-4. Hydrogen isotope analyses of Peregrine Falcon feathers. Results listed in δD ‰.

	Natal Down Mean ± 1 SD	Juvenile Down Mean ± 1 SD	Juvenile Plumage Mean ± 1 SD	Change 1*	Change 2ǀ
Control Group					
E (*n* = 3)	-146 ± 6	-145 ± 5	-145 ± 7	+1	0
A (*n* = 3)	-143 ± 3	-141 ± 1	-142 ± 3	+2	-1
Whole Group (*n* = 6)	-144 ± 4	-143 ± 4	-144 ± 5	+1	-1
Treatment Group					
B (*n* = 3)	-143 ± 1	-122 ± 4	-118 ± 4	+21	+4
C (*n* = 2)	-141	-118	-117 ± 5	+23	+1
D (*n* = 2)	-139	-116	-113 ± 0	+23	+3
Whole Group (*n* = 7)	-141± 2	-119 ± 4	-116 ± 4	+22	+3

*Change 1 is the difference between natal down and the juvenile down

ǀChange 2 is the difference between the juvenile down and juvenile plumage



Japanese Quail		Peregrine Falcons	
Breeding Adults Provided with D-enriched food and water for five weeks prior to sampling hatchlings		**Breeding Adults** Kept on regular diet of D-depleted quail and water	
Treatment Group With Diet Switch ($n = 30$)	Control Group Without Diet Switch ($n = 30$)	Treatment Group With Diet Switch (Groups B, C, D, $n = 7$)	Control Group Without Diet Switch (Groups A, E, $n = 6$)
Provided with D-depleted food and water	Provided with D-enriched food and water	Provided with D-enriched Quail from control group and D-enriched water	Provided with D-depleted quail and water
δD values are expected to change between plumage stages	δD values are not expected to change between plumage stages	δD values expected to change through plumage stages	δD values are not expected to change between plumage stages

Figure 2-1. The relationship between experimental groups of quail and falcons. The darkened area indicates the groups provided with D-enriched food and water.

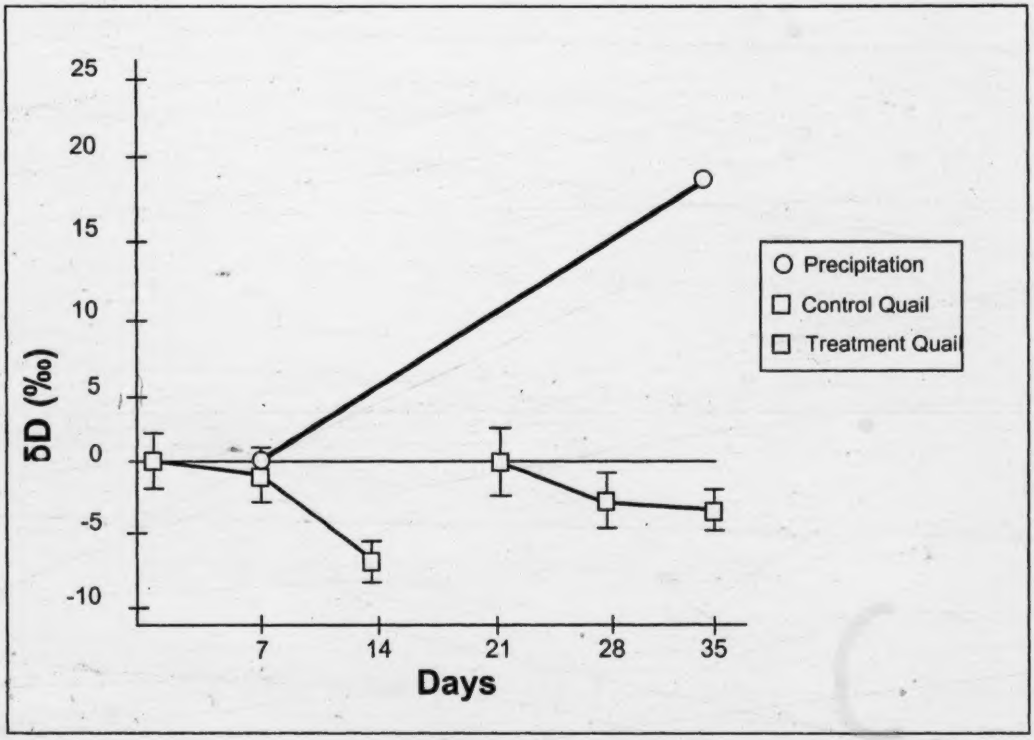


Figure 2-2. A comparison between a potential change in δD values of the precipitation and the initial δD values of multiple groups of quail. The lines for the quail plot the relative change between mean δD values of each batch of newly hatched quail in the control and treatment groups. Error bars for quail represent ± 1 SD.

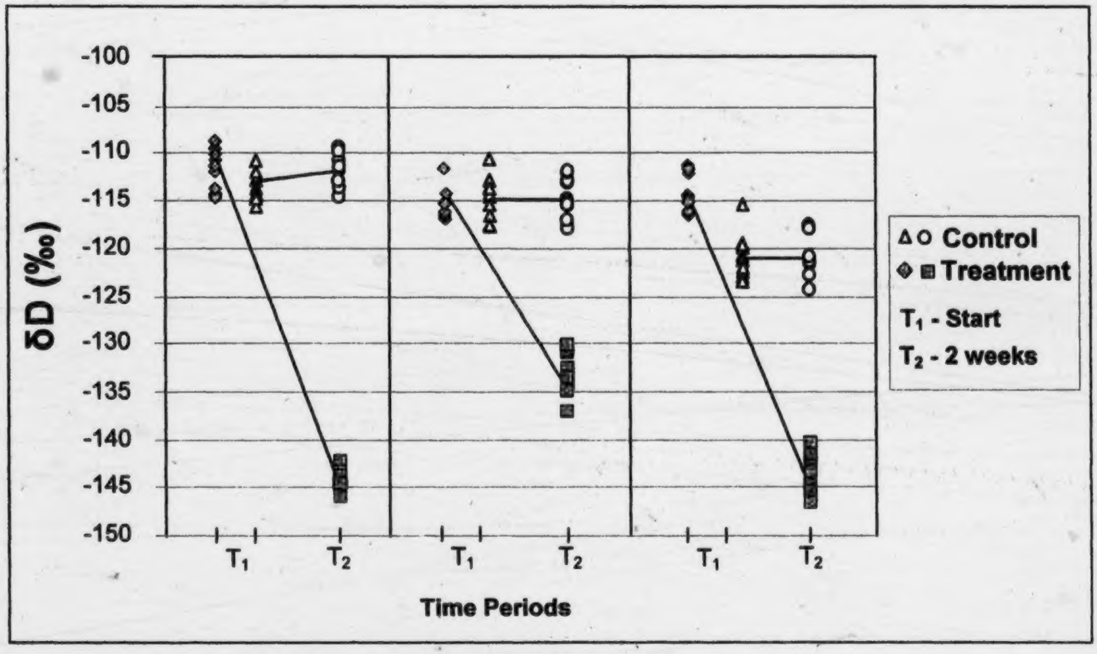


Figure 2-3. The effects of a diet switch on δD values in Japanese Quail feathers. The three pairs of data points represent batches of quail.

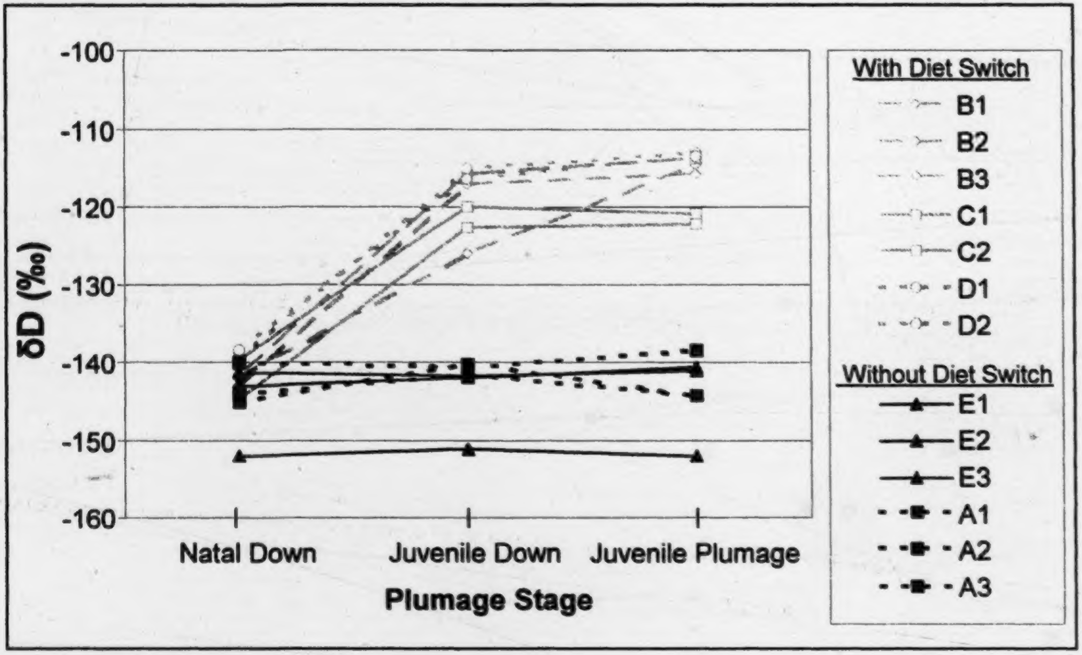


Figure 2-4. The effects of a diet switch on δD values in Peregrine Falcons feathers.

Literature Cited

[1] Hobson KA (1999a) Tracing origins and migration of wildlife using stable-isotopes: a review. *Oecologia* **120**, 314-326

[2] Caccamise DF, Reed LM, Castelli PM, Wainright S, and Nichols TC (2000) Distinguishing migratory and resident Canada Geese using stable isotope anaysis. *Journal of Wildlife Management* **64**, 1084-1091

[3] Chamberlain CP, Bensch S, Feng X, Akensson S, and Andersson T (2000) Stable-isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus* and *Pylloscopus trochilus acredula*) reflect their African winter quarters. *Proceedings of the Royal Society of London* **267**, 43-48

[4] Hobson KA, Brua RB, Hohman WL, and Wassenaar LI (2000) Low frequency of "double molt" of remiges in Ruddy Ducks revealed by stable-isotopes: implications for tracking migratory waterfowl. *Auk* **117**, 129-135

[5] Hobson KA, McFarland KP, Wassenaar LI, Rimmer CC, and Goetz JE (2001) Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. *Auk* **118**, 16-23

[6] Meehan TD, Lott CA, Sharp ZD, Smith RB, Rosenfield RN, Stewart AC, and Murphy RK (2001) Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. *Condor* **103**, 11-20

[7] Rubenstein DR, Chamberlain CP, Holmes RT, Ayres MP, Waldbauer JR, Graves GR, and Tuross NC (2002) Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. *Science* **295,** 1062-1065

[8] Hobson KA, Wassenaar LI, and Taylor OR (1999) Stable-isotopes (δD and δ^{13}C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oegologia* **120**, 397-404

[9] Wassenaar LI and Hobson KA (1998) Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proceedings of the National Academy of Science* **95**, 15436-15439

[10] Chamberlain CP, Blum JD, Holmes RT, Feng X, Sherry TW, and Graves GR (1997) The use of isotope tracers for identifying populations of migratory birds. *Oecologia* **109**, 132-141

[11] Hobson KA and Wassenaar LI (1997) Linking breeding and wintering grounds of neotropical migration songbirds using stable isotopic analysis of feathers. *Oecologia* **109**, 142-148

[12] Hobson KA and Wassenaar LI (2001) Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. *Ecological Applications* **11**, 1545-1553

[13] Mizutani H, Fukuda M, Kabaya Y, and Wada E (1990) Carbon isotope ratio of feathers reveals feeding behaviour of cormorants. *Auk* **107**, 400-403.

[14] Hobson KA (1999b) Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. *Condor* **101**, 799-805

[15] Hobson KA (2002) Science's Compass: Incredible journeys. *Science* **295**, 981-982.

[16] Wassenaar LI and Hobson KA (2001) A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology* **35**,1845-1850.

[17] Alibardi L (2002) Keratinization and lipogenesis in epidermal derivatives of the Zebra Finch, *Taeniopygia guttata castanotis* (Aves, Passeriformes, Ploecidae) during embryonic development. *Journal of Morphology* **251**, 294-308.

[18] Herbert RA and Herbert KGS (1965). Behavior of Peregrine Falcons in the New York City region. *Auk* **82**, 62-94.

[19] Johnson-Beaver L (1979) Biology and management of Peregrine Falcons (*Falco peregrinus*) in northwestern Alberta. Alberta Oil Sands Environmental Research Program, Project LS 22.3.1, 94 pp.

[20] Prum, RO and Williamson, S (2001) Theory of the growth and evolution of feather shape. *Journal of Experimental Zoology* **291**, 30-57.

[21] Klaassen M, Lindstrom A, Meltofte H, and Piersma T (2001) Arctic waders are not capital breeders. *Nature* **413**, 794.

[22] Atwell L (2000) Using stable carbon and hydrogen isotopes to examine nutrient allotment by breeding Redhead Ducks. MSc. Thesis, University of Saskatchewan, Saskatoon, Saskatchewan. 113 pp.

[23] Ryder JP (1970) A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bulletin* **82,** 5-13.

[24] Court GS, Gates CC, Boag DA, McaNeil JD, Bradley DM, Fesser AC, Patterson JR, Stenhouse GB, and Oliphant LW (1990). A toxicological assessment of peregrine falcons (*Falco peregrinus tundrius*) breeding in the

Keewatin District of the Northwest Territories, Canada. *Canadian Field-Naturalist* **104**, 255-272.

[25] Hobson KA (1995) Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: Patterns of isotopic fractionation and turnover. *Condor* **97**, 752-762.

[26] Hobson KA, Atwell L, and Wassenaar LI (1999) Influence of drinking water and diet on the stable isotope ratios of animal tissues. *Proceedings of the National Academy of Science* **96,** 8003-8006.

[27] Hobson KA and Clark RC (1992a). Assessing avian diets using stable-isotopes I: Turnover of ^{13}C in tissues. *Condor* **94**, 176-186.

[28] Hobson KA and Clark RC (1992b). Assessing avian diets using stable-isotopes II: Factors influencing diet-tissue fractionation. *Condor* **94**, 189-197.

[29] Hobson KA and Wassenaar LI (1999) Stable isotope ecology: an introduction. *Oecologia* **120**, 312-313.

[30] Estep MF and Dabrowski H (1980) Tracing food webs with stable hydrogen isotopes. *Science* **209**, 1537-1538.

[31] Deniro M and Epstein S (1981) Hydrogen isotope ratios of mouse tissues are influenced by a variety of factors other than diet. *Science* **214**, 1374-1375.

[32] Cormie AB, Schwarcz HP, and Gray J (1994) Relationship between hydrogen isotopic ratios of bone collagen and rain. *Geochimica Comochimica Acta* **58**, 377-391.

[33] Schimmelmann A (1991) Determination of the concentration and stable isotopic composition of non-exchangable H in organic matter. *Analytical Chemistry* **63**, 2356-2459.

[34] Wassenaar LI and Hobson KA (2000) Improved method for determining the stable-hydrogen isotopic composition (δD) of complex organic materials of environmental interest. *Environmental Science and Technology* **34**, 2354-2360.

[35] Global Network of Isotopes in Precipitation (GNIP) and Isotope Hydrology Information System (ISOHIS). http://isohis.iaea.org

[36] Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187-211.

[37] Venneman TW and O'Neil JR (1993) A simple and inexpensive method of hydrogen isotope and water analysis of minerals and rocks based on zinc reagent. *Chemical Geology* **103**, 227-234.

[38] U.S. Fish and Wildlife Service. 2003. Monitoring Plan for the American Peregrine Falcon, A Species Recovered Under the Endangered Species Act. U.S. Fish and Wildlife Service, Divisions of Endangered Species and Migratory Birds and State Programs, Pacific Region, Portland, OR. 53 pp.

[39] Bearhop S Waldron S Votier SC, and RW Furness (2002) Factors influencing assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* **75**: 451-458.

Chapter 3

Remote monitoring of Peregrine Falcons with stable-isotope analysis of hydrogen, carbon and nitrogen ratios in feathers[2]

The North American Peregrine Falcon (*Falco peregrinus*) research and conservation community has succeeded in returning populations to a state where the falcon could be down-listed or de-listed on endangered/threatened species lists (USDI 1994, USDI 1999, COSEWIC 2000). The recovery of Peregrine Falcon populations is the result of over 30 years of intensive conservation research and monitoring. Continental scale surveys played an important role in the monitoring of the decline and recovery of the falcon populations. At the 1969 Raptor Research Planning Conference at Cornell, it was decided that as many of the North American populations would be surveyed every 5 years commencing in 1970 (Kiff 1988). The early surveys determined the existing status of the populations and subsequent surveys measured recovery of populations across North America.

For the first few survey years, the number of regions investigated increased, allowing for searches that were more thorough and the exploration of areas not previously searched. The surveys were conducted for populations of all three North America sub-species *Falco peregrinus anatum, Falco peregrinus tudrius*, and *Falco peregrinus pealei*. The 1970 survey was limited to northerly regions of North America that were classified into 15 large, generalized areas

---

[2] *This chapter has been formatted for submission to the Journal of Raptor Reasearch*

(Cade and Fyfe 1970). The survey of 1975 was conducted with greater participation and resources in 35 regions across the whole of North America (Fyfe et al. 1976). By 1980, 52 regions were surveyed that included new areas in the central Arctic not previously searched (White et al. 1990).

Once some populations were on the way to recovery, the survey effort in those populations began to decline. The continental surveys were regionalized into jurisdictional surveys in 1985/86 (Bromely 1988, Bromley and Matthews 1988, Mattox and Seegar 1988, Mossop 1988, Murphy 1990). The amount of effort and resources going towards surveying the Arctic populations were scaled back (Peakall 1990). Only select areas were monitored across the whole range of Arctic breeding Peregrines and protocols in the many of the regions surveyed no longer included ground searches and nest visits. Aerial surveying became the primary method of monitoring (Bromley and Matthews 1988, Holroyd and Banasch 1996, Rowell et al. 2003, Banasch and Holroyd *in press*).

A method of remotely monitoring North American populations of Peregrine Falcons is desirable. Travel in the Arctic is very expensive and many Peregrine Falcon populations are isolated. Eyries within populations can be scattered across large areas. A method of monitoring multiple populations from a single, easily accessible point would be more cost effective and practical.

The application of leg bands for mark-recapture studies involves expensive fieldwork in remote areas. The rarity of band recoveries is one of the limitations of mark-recapture studies, requiring decades to establish migratory pathways and population indices. The frustrations associated with traditional mark-recapture methods are being alleviated by new or improved techniques. The application of the relatively new technique of stable-isotope analysis (SIA) is an alternative that can be used where previous attempts to delineate populations using genetic markers found limited success (e.g. isozyme polymorphisms [Morizot 1988] or DNA restriction fragment length polymorphisms [Longmire 1988]).

Naturally occurring continental patterns in stable-isotope ratios have been used to delineate geographic regions and track migrants to the general area where individuals bred or hatched (Alisauskas and Hobson 1993, Chamberlain et al. 1997, Hobson and Wassenaar 1997, Caccamise et al. 2000, Chamberlain et al. 2000, Hobson and Wassenaar 2001, Wassenaar and Hobson 2001, Kelly et al. 2002, Rubenstein et al. 2002). However, without extensive ground-truthing, estimations of the origins of migrants were too generalized to separate adjacent populations of most species studied to date. An improvement to tracking migratory animals with isotopes came with the division of the process into two components. The first was the creation of a con-specific stable-isotope map, database or model. The determination of the stable-isotope signature of migrants that were then compared to the map, database or model was the second step (Wassenaar and Hobson 1998, Hobson et al. 1999, Cherel et al.

2000, Hobson et al. 2000, Hebert and Wassenaar 2001, Hobson and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001).

The greatest accuracy in delineating the origins of migrants has been demonstrated by studies that were able to obtain natal samples from the majority of the breeding range (Wassenaar and Hobson 1998, Hobson et al. 1999, Hobson et al. 2001). The determination of the regional differences in isotopic signatures throughout the majority of a species' range, rather than interpolation with the use of a model, increases the accuracy of predicting values for areas not sampled for the creation of a reference dataset. Once the isotopic values of natal tissues are known across the range of a species, migrants caught along their migration routes or on their wintering grounds can be sampled for tissues presumably grown on their natal / breeding grounds. The relative proportion of migrants originating from different parts of their range can then be determined.

SIA was used to delineate regions of breeding Peregrine Falcons and to determine the origins of Peregrines at a specific migration site. Raptor banding programs have shown that there are areas in the United States where Peregrine Falcons are concentrated on their fall migrations (Anderson et al. 1988, Ward et al. 1988, Yates 1988). Padre Island, Texas was chosen to take advantage of a long-term Peregrine Falcon study that includes the capture of passage falcons in the autumn (Yates et al. 1988). Band recoveries indicate that this region of the Gulf Coast of Texas is an area where western and central Arctic-bred falcons were known to pass en route to wintering grounds (Yates et al. 1988). Banding studies indicate that the greater part of banded Peregrines that are re-trapped on Padre Island originated in Alaska (Yates et al. 1988). However, this may be a measure of banding effort as the frequency of banding nestlings has decreased to almost none in the Canadian Arctic (Bromley and Matthews 1988, Holroyd and Banasch 1996). Padre Island was considered an excellent location for this investigation of SIA as an option to remotely monitor northern Peregrine Falcons.

With the use of stable-isotope tracking, the proportions of Peregrine Falcons from different geographic locations that passed through the Padre Island migratory site were determined. The goal was to determine the site's importance to falcons that originate in northern North America; areas of the Arctic that are expensive to monitor through rigorous surveys. The first objective of this study was to use stable-isotope analyses of natal Peregrine Falcons feathers collected across northern North America to delineate regions by differences in their stable-isotope signatures. The separation of the collection areas by isotopic signatures is best accomplished with the investigation of multiple elements (Chamberlain et al. 1997). The greater the number of elements used, the higher the probability regions will have different isotopic signatures. For this study, the ratios of hydrogen, carbon and nitrogen stable-isotopes in feathers were examined. Once the falcon feather collection areas were isotopically distinguished, the second objective was to determine the origins of fall-passage, young-of-the-year falcons.

METHODS

Sample Collection – Nestlings. Beginning in 1995, volunteer researchers collected feather samples from nestling Peregrine Falcons in ten provinces/territories across Canada, seven states from the United States of America, and the south west coast of Greenland during visits to count and band nestlings (Table 3-1, Fig. 3-1). Feather samples were collected from multiple collection sites in some provinces and states. The sample size obtained from each region reflected the effort to visit nests in the various populations across the continent.

Many nest sites are remote and had few visits, so the age at which the nestlings were sampled varied from site to site. Thus, consistent feather types were not collected at each site. A juvenile-plumage body feather was optimal, however, samples of juvenile-down and natal-down were all that were possible in some instances due to the young age of the nestlings. Juvenile-plumage feathers and juvenile-down were the optimal choice for the analyses. Due to biases associated with isotopic signals in nutrients from maternal sources in egg formation (Duxbury et al. 2003), the analysis of natal-down feathers was conducted unless no other feathers were available. However, given the extensive range of Peregrine Falcons, this study represents one of the most comprehensive sampling efforts for isotope-tracking of any species to date.

Sample Collection – Migrants. Any feathers grown by young-of-the-year falcons represents the location from where they fledged since the nutrients used to grow the feathers were provided at the nest. Axillary feathers were collected from autumn passage, young-of-the-year Peregrine Falcons that were trapped on Padre Island, Texas in October and November 1999, 2000, 2001 (Fig. 3-1).

Feather Analyses. Feathers were first washed with a mild solution of detergent and water. Surface oils and contaminants were removed with a 2:1 solution of chloroform and methanol. Feathers washed with the solution were allowed to dry in a fume hood before samples were measured. Between 7-10 mg of feather tissue were required for hydrogen analyses, and another 1 mg was required for the carbon and nitrogen analyses. In most cases, the amount of feather tissue provided allowed for the use of one feather for both analyses. However, some feathers from nestlings were too small to use for both analyses. In those situations, separate feathers had to be used for the two analyses. It was assumed that the isotope values in feathers grown on the same nestling during the same time frame were identical.

Hydrogen. Feathers are almost completely composed of keratin protein. Most of the hydrogen in keratin is bonded to carbon atoms by strong covalent bonds. However, hydrogen atoms are also weakly bonded to the nitrogen and oxygen atoms of the protein molecules. The weak bonds can lead to exchange with hydrogen in ambient water vapour (Schimmelmann 1991). This exchange can introduce erroneous migration-tracking results associated with the transport and storage of samples away from the site where the feathers were grown.

To control the effects of this exchangeability of hydrogen, samples were equilibrated under controlled conditions using a modified method similar to those developed by Schimmelmann (1991) and Wassenaar and Hobson (2000). With the use of a steam chamber, the samples were exposed to water vapour with a known hydrogen isotopic value at 130°± 0.1C for a period of two hours. The samples were then allowed to slowly return back to room temperature. Samples were sealed under vacuum and combusted at 850°C for two hours, and were gradually allowed to return to room temperature. The resulting water vapour was reduced to H_2 gas over hot zinc. Hydrogen from the feather samples was analyzed with the use of a duel-inlet, Finnigan-MAT 252 mass spectrometer. Hydrogen isotopic values are reported as δD values and are in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. Results were normalized using a scale of standards (VSMOW/GISP/SLAP). Water samples analyzed with each batch of feathers produced a 95% confidence interval of ± 1‰ (n=54). An isotopic fractionation factor of +80‰ was used in calculating the δD values of the non-exchangeable hydrogen (D_n)(equation 2, Hobson et al. 2001). Samples were equilibrated and analyzed randomly in order to minimize the introduction of temporal and isolation biases (Hurlbert 1994).

Carbon and nitrogen. From the same part of each feather, a one mg sample was collected and placed in a tin cup and was combusted in a Robo-Prep elemental analyzer at 1800°C. The resultant CO_2 and N_2 were analyzed with the use of an inter-faced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS). Carbon isotope ratios ($\delta^{13}C$) are expressed relative to the PeeDee Belemite (PDB) international standard. Nitrogen isotope ratios ($\delta^{15}N$) are expressed relative to atmospheric N_2. Analytical error was measured at ± 0.1‰ and ± 0.3‰ for stable-carbon and nitrogen isotope measurements respectively.

Statistical Analyses. A multivariate General Linear Model procedure (GLM) was used to determine if significant variability existed among the isotopic values of the natal feathers across the geographic range of the study. The samples were categorized by collection areas. Each element (H, C, N) was analyzed separately and grouped into homogenous sub-sets of isotopic values by a post-hoc Tukey's HSD (α=0.05). Unique combinations of sub-sets from the three Tukey's HSD analyses were used to differentiate the collection areas. A discriminate function analysis (DFA) was used to test how well the feather samples could be associated with collection sites (Wassenaar and Hobson 2000). To determine if a linear relationship existed between hydrogen and carbon isotope values in the natal feathers, a regression was conducted with δD_n values against $\delta^{13}C$ values. Once the isotope dataset was created, the natal origins of young-of-the-year migrants were estimated by a comparison of the isotope values of the migrant feathers to the parameters of the isotopically delineated collection areas. Statistical analyses were conducted using SPSS v.11.

RESULTS

Natal Feather Analyses. The inaccessibility of most Peregrine Falcon eyries compounded with the high number of volunteers (24) who collected feathers for this study produced some inconsistency in the feather type collected. Of the feather samples collected, 171 from 39 collection areas met the criteria for juvenile down and juvenile plumage feathers to create an isotope reference dataset (Duxbury et al. 2003). Sixty-nine (40%) samples of juvenile down had to be used in the creation of the dataset. The use of natal-down feathers can be problematic since endogenous maternal nutrients may be used to form these feathers (Duxbury et al. 2003). The isotopic signature of natal-down may be reflective of an adult female's wintering grounds and not the local isotopic signature (Duxbury et al. 2003). Nineteen (11%) natal down samples were analyzed with caution from collection sites where few juvenile down and body feathers were collected. The remaining 83 (49%) samples were from nestling juvenile plumage (body feathers, or small samples from flight feathers). The rejection of most of the natal-down samples led to some collection regions being represented by small sample sizes (Table 3-1).

The variability of sibling SIA results was comparable to multiple runs of a standard. Generally, the variance of isotope values between sampling areas was greater than the variance of isotope values within sampling areas across the continental range of the study (GLM *Pillai's Trace* $F_{25,151} = 12.196$, $P<0.0001$). However, the standard deviation of a few collection areas was relatively large (Table 3-2). The sample mean δD_n values ranged from -180‰ to +48‰ (GLM $F_{25,147} = 64.385$, $P<0.0001$) (Table 3-2). Three collection areas with probable coastal breeding falcons (Langara Island, BC; Oregon; and Greenland) had samples with very enriched δD_n values that are associated marine food webs (Lott et al. 2003). With the exclusion of populations of coastal nesting falcons, the variability of isotope values between sampling areas remained significant, ranging from -180‰ to –51‰ (GLM $F_{23,144} = 44.671$, $P<0.0001$). Regions of the south-east portion of North America generally had relatively enriched δD_n values, while areas towards the north-west had relatively more depleted δD_n values. Known patterns of δD in precipitation predict that Arctic areas west of the Rocky Mountains will have similar δD values as other areas east of the mountains due to the fractionation effects associated with changes in altitude (Kharaka and Carothers 1980, Sheppard 1986, Hobson and Wassenaar 1997). These patterns appear to be reflected in the hydrogen isotope values of the falcon nestlings as the northwest depletion trend was reversed in Alaska samples. The δD_n values of collection areas on the western side of the Rocky Mountains in Alaska are similar to those east of the Rockies. The δD_n values from the northern portion of the state had a mean value similar to an Arctic region east of the Continental

Divide. The expected depletion between δD values of precipitation and the δD_n values of feathers (Cormie et al. 1994, Wassenaar and Hobson 2001) ranged from approximately 20-40‰ depending on the location of the sample collection site.

The range of mean $\delta^{13}C$ values was also considerable across the study areas (-24.5 to -16.2‰)(GLM $F_{25,140} = 16.917$, $P<0.0001$). As with the δD_n values, the $\delta^{13}C$ values also fell into a gradient with relatively more depleted values associated with the northern collection areas (Table 3-2). A significant relationship was found between the δD_n and $\delta^{13}C$ values across the continental range of the study ($F_{1,23} = 44.67$, $P < 0001$, $r^2 = 0.49$; Fig. 3-2).

While mean $\delta^{15}N$ values significantly differed between regions (GLM, $F_{25,140} = 17.900$, $P<0.0001$), a gradient was not apparent across the study areas. However, the discriminate function analysis indicated that nitrogen used in conjunction with hydrogen and carbon, was the most effective in separating samples across the study area. The DFA correctly classified 70% of the samples to their collection sites by using a combination of D_n, ^{13}C and ^{15}N.

The post-hoc Tukey's HSD grouped the δD_n, $\delta^{13}C$ and $\delta^{15}N$ values into 7, 3 and 3 homogenous sub-sets respectively (Table 3-2). The δD_n values had two sub-sets with only one value in each. The $\delta^{15}N$ values had one sub-set consisting of only a single value. A decrease in the number of sub-sets indicated a decrease in variability in the isotope species across the study range. Hydrogen had the greatest variability between and within collection areas. The greater variability was a reflection of a larger range of values across North America as compared to carbon and nitrogen values. The three sets of Tukey's classifications were then combined for each region. Regions with matching combinations of Tukey's classifications were categorized into groups lettered A-M (Table 3-2, Fig. 3-1). Due to distinctive marine isotope signatures, the three collection areas with coastal breeders were lettered X-Z.

Migrant Tracking. The 105 samples from migrant, hatch-year falcons consisted of 18 samples drawn from the 1996 collection, 38 from the 2000 collection and another 49 from the 2001 collection. The migrant falcon isotope values were grouped using the same alpha-code categories used in the creation of the dataset. Thirty-eight samples (36.2%) had δD_n, $\delta^{13}C$ and $\delta^{15}N$ values that fell within a standard deviation the mean isotope values that demarcated a collection area. Twenty-six of those 38 samples were associated with collection areas with relatively depleted δ D_n and $\delta^{13}C$ values (Fig. 3-3).

The remaining 67 of the original 105 samples had at least one element outside the parameters of the sample sites. The origins of these remaining samples were estimated with the use of the linear relationship between δD_n and $\delta^{13}C$ and plots of the standard deviations surrounding the alpha-code classifications (Fig. 3-4). Of the 67 samples, 40 fell within the boundaries of at least one collection area. Specificity in some instances was limited due to overlapping standard deviations of δD_n or $\delta^{13}C$ values of some sampling locations (Fig. 3-4). The other 27 of the 67 samples had δD_n and $\delta^{13}C$ values that fell outside of the sampling site parameters, but the majority were relatively depleted of both D_n and ^{13}C. Of the 67 samples plotted by their δD_n or $\delta^{13}C$ values to estimate their origins, the majority had relatively depleted δ D_n and $\delta^{13}C$ values (Fig. 3-4).

DISCUSSION

With the use of stable-isotope analysis, regions of Peregrine Falcons across northern North America were demarcated. The δD isotopic gradients of the falcon feathers generally followed latitudinal patterns similar to those of isotope base-maps created by Wassenaar and Hobson (2000), Hobson and Wassenaar (2001), Hobson et al. (2001) and Meehan et al. (2001). Not unlike previous studies, the δD_n values of some sample locations did not seem to "fit" geographically (Fig. 3-1) given the established relationship between the δD in precipitation and δD of feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Hobson and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001, Rubenstein et al. 2002). The relatively enriched δD_n values of the Brandon, MB site (Table 3-2) are probably caused by the reliance of natal down feathers for the site. Natal down reflects nutrients derived partially from maternal, endogenous sources, which may be indicative of food sources digested on migration or on the winter grounds (Duxbury et al.

2003). This explanation cannot be used for the Wood Buffalo National Park collection sites, which also had relatively enriched δD_n values. Feathers sampled for this region were either juvenile down or juvenile body feathers, which should reflect the isotopic signature of local food systems. In addition, because the samples were analyzed in a random order, the anomaly should not have been caused by temporal or isolation biases. At this time, it is uncertain whether the cause was due to microclimatic or dietary effects. The cause of the relatively large standard deviations of some collection areas is also unclear. However, one area with a large standard deviation was Langara on the coast of British Columbia. The δD_n values in coastal regions can vary greatly depending if the diet is marine or terrestrial based (Meehan et al. 2001, Lott et al. 2003).

The relative proportion of plants that use different photosynthetic pathways across North America causes a continental gradient in $\delta^{13}C$ values. Differences stable-isotope ratios in plants can be caused by temperature dependent fractionation events in enzymatic reactions, as well as differences in water use efficiency at varying levels of relative humidity (Körner et al. 1991, Lajtha and Marshall 1994, Hobson and Wassenaar 2001, Rubenstein et al. 2002). The continental gradient in the $\delta^{13}C$ values of natal feathers of this study is important because it supports previous descriptions of latitudinal patterns in carbon isotope ratios (Chamberlain et al. 1997, Wassenaar and Hobson 1998, Hobson et al. 1999, Hobson and Wassenaar 2001, Rubenstein et al. 2002). However, such a gradient is not always apparent (Hobson et al. 2001, Wassenaar and Hobson 2001, Graves et al. 2002) and may be species specific. The gradient could be correlated with dietary preferences of the study species. For example, the highly variable diet of Peregrine Falcons includes many types of prey. The plants and animals of the falcons' food webs across its range could be indicative of $\delta^{13}C$ values that change with latitude. Other species may focus on specific foods with similar physiology and $\delta^{13}C$ values across their range, thus potentially masking a gradient. A more simple explanation may be whether the study species had an extensive enough range in which relative changes in $\delta^{13}C$ values could be detected (Chamberlain et al. 1997, Wassenaar and Hobson 2001, Rubenstein et al. 2002). While the basis may be unclear, the fact that there was a $\delta^{13}C$ gradient in this study validates the investigation of carbon isotopes in the determination of migratory patterns.

The $\delta^{15}N$ values of animals in eastern Africa differ from those of animals in western Africa (Van der Merwe et al. 1990, Vogel et al. 1990, Chamberlain et al. 2000). Geographical patterns of nitrogen isotopes are related to the relationship between the enrichment of $\delta^{15}N$ values and an increase in aridity and denitrification (Shearer et al. 1978). Theoretically, a continental gradient for $\delta^{15}N$ values could be possible across North America with relatively higher $\delta^{15}N$ values associated with arid regions in the southwest. A continental gradient was not expected in this study because of the lack of Peregrine feather collection areas in the southwest of North America. At a smaller scale, nitrogen isotope ratios in food webs vary due to the existence of various sources of nitrogen with different isotope values. The stable-isotope ratios of these various sources of nitrogen are altered by a variety of plant species that use assorted nitrogen fixing strategies that fractionate isotopes differently (Schulze et al. 1994, Michelsen et al. 1996). Soils may also become relatively enriched in ^{15}N in areas associated with intensive agricultural practices (Duxbury 1998, Hebert and Wassennaar 2001). The resultant stable-isotope ratios can be altered again depending upon how many trophic levels exist below the study species, since metabolism/catabolism leads to a depletion of lighter isotopes in predators (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1992, Hobson 1993). With many sources of variability and the lack of feather collection in the southwest of North America, predictable patterns in $\delta^{15}N$ values across the sampling range were not expected. However, the inclusion of the nitrogen stable-isotope ratios allowed for greater differentiation of collection areas than what was possible with only δD_n and $\delta^{13}C$ values.

Peregrine Falcon Monitoring. The occasional Peregrine Falcon band recovery at Padre Island can provide direct evidence of a link between the Gulf Coast migration route and the banding site (Anderson et al. 1988, Ward et al. 1988, Yates 1988). The rarity of such recoveries is one of the drawbacks of this conventional method of monitoring populations and migrations. Of the 36,836 Peregrines banded between 1955-2002, only 2779 (7.5%) have been recovered (USGS 2003). In addition, band recoveries from the majority of the Northwest Territories are not possible due the lack of Peregrine Falcon banding projects.

While satellite telemetry provides a precise method of tracking the movements of Peregrine Falcons (Fuller et al. 1998, Holroyd and Duxbury 1999), the expense and logistics of the technology severely limits sample sizes (Hobson 2002). While stable-isotope tracking cannot provide the exact summer origin where a migrant Peregrine fledged, the general region can be estimated for every trapped falcon. If Peregrines can be traced to areas with unique isotope values, the proportion of migrants that originate from various collection areas and subsequently pass through a migration site can be determined. SIA presents a potential method for remotely monitoring falcons in northern regions where Peregrines are not banded or no longer being intensely monitored. Therefore, the time required to accumulate enough migratory data to discern meaningful patterns can be reduced from decades to a few banding seasons.

Based on bird captures, bird populations are monitored with the creation of indices (Dunn et al. 1997, Francis and Hussell 1998, Link and Sauer 1998). SIA can make bird captures more informative by geo-referencing the indices with an estimate of the origin of the captured birds. The capture of unbanded falcons can only indicate whether Peregrine Falcon numbers as a whole are increasing or decreasing. With knowledge of where each captured falcon originated, individual regions could be monitored for changes. If adult and hatch-year falcons were caught in a standardized method, a ratio of juveniles to adults could be computed and the productivity of individual populations could potentially be determined.

The results of this study indicate an important link between Padre Island and western populations of Peregrine Falcons. The majority (61.0%) of the total 105 feathers from Padre Island migrants appear to have originated in the western Arctic. Between 29 (27.6%) and 38 (36.1)% of the total migrants appear to have had origins in Alberta, Saskatchewan, and north to Rankin Inlet. Of the total 105 migrant samples, between 11 (10.5%) and 14 (13.3%) had possible origins east of 102° W and south of Rankin Inlet, NU (Figure 3-1, 3-3, 3-4). One sample fell within the parameters of southwest Greenland (Figure 3-4).

Other Migration Routes. Satellite data from Alberta indicates that most Peregrine Falcons in Alberta probably use the Gulf Coast flyway to migrate to their winter grounds (G. Holroyd unpubl. data). However, other falcons were satellite-tracked to the Pacific flyway and the Atlantic flyway. The SIA results indicate a heavy western bias to the Padre Island migrants, which implies eastern populations of breeding falcons use other migration routes. For accurate monitoring of Peregrine Populations, the relative use of other flyways would first have to be determined. The isotope reference data compiled in this study can now be used in the application of stable-isotope tracking to other Peregrine Falcon migration sites such as those on the east and west coasts. The majority of the far western breeding Peregrines may be using a west coast migration route (Anderson et al. 1988). Feathers have been obtained from a west coast migration site in hopes of determining the summer origin of falcons using this flyway. What is currently lacking is a reference dataset of multiple breeding sites along the west coast. The δD, δ^{15}N and δ^{34}S values in bird feathers derived from marine systems are significantly different and these unique signatures could be used to delineate regions of coastal nesting Peregrine Falcons (Fry 1988, Hobson et al. 1997, Caccamise et al. 2000, Lott et al. 2003). Since marine sulphur sources (sulphates) can be 30‰ more enriched than terrestrial sources (sulphides; Michener and Schell 1994), the addition of sulphur analysis for the delineation of west coast breeding areas would be advantageous.

ACKNOWLEDGEMENTS

I would like to thank L. Priestley, D. Birn and M. Wendlant for their assistance in the lab. Many thanks go to the feather collectors because without them, this study would not have been possible: G. Holroyd, S. Ambrose, D. Mossop, K. Hodson, C. Shank, M. Bradley, J. Dixon, G. Court, D. Stepnisky, L. Priestley, J. Folinsbee, W. Nelson, P. Thompson, L. Olyphant, R. Jones, B. Ratcliff, T. Armstrong, M. LePage, and B. Mattox, A. Grøngaard, J. Pagel, M. Martell, D. Amirault, and P. Hunter. Also, thanks to Environment Canada's Stable-isotope Laboratory for running the C&N analyses. I am grateful to H. Trefry for completing the permit application process, and MK. Skoruppa for organizing and shipping feathers from the US. I am also grateful to W. Calvert for providing laboratory space at the Canadian Forestry Centre Edmonton during the early years of this project. Special thanks go to G. Holroyd of the Canadian Wildlife Service for his endless logistical and financial support. Special thanks also go to K. Muehlenbachs of the Department of Earth and Atmospheric

Sciences at the University of Alberta for his guidance in stable-isotope analysis, and for providing laboratory space and in-kind support. Approval for this project was provided by the Animal Care Committee of the Canadian Wildlife Service. Finally, I am grateful to Environment Canada; the Natural Sciences and Engineering Research Council of Canada; Alberta Sports, Recreation, Parks, and Wildlife Foundation; and the University of Alberta for funding this project.

Table 3-1. Collection sites for nestling Peregrine Falcon feather samples. Individuals (n) were analyzed for each nest unless the amount of sample from an individual was inadequate for analysis. Feathers from multiple individuals were pooled to obtain adequate amounts of sample.

Site	Latitude	Longitude	*n*
British Columbia			
Langara Island	54.200	-133.000	4
Alberta			
Wood Buffalo National Park	59.134	-112.433	10
Central Alberta	53.573	-113.821	10
South-Central Alberta	51.653	-113.480	11
Saskatchewan			
Saskatoon*	52.167	-106.667	6
Regina*	50.500	-104.633	5
Manitoba			
Brandon*	49.917	-97.167	5
Winnipeg*	49.883	-100.300	3
Ontario			
London	42.967	-81.250	9
Toronto Region	43.528	-79.583	14
Thunder Bay Region	48.487	-75.717	8

Ottawa	45.417	-89.057	5
Quebec			
Lac Sault*			2 (pooled)
Cap-Tourmente*	47.700**	-73.500**	1 (pooled)
La Baie Anse a Poulette*			2 (pooled)
New Brunswick			
Hillsborough			1 (pooled)
Owl's Head*	45.717**	-64.815**	5
Edgett's Landing*			2
Yukon			
White River Region	62.850**	-140.250**	4
Yukon River Region	63.750**	-139.250**	6
Porcupine River Region	66.800**	-139.250**	6
Northwest Territories			
MacKenzie River Region	71.024**	-118.909**	9
Nunavut			
Rankin Inlet	62.750	-92.167	10
Alaska			
Sagavanirktok River Region	69.372**	-148.649**	6
Colleville River Region	69.919**	-151.592**	2
Oregon			
	43.150	-124.133	1
Iowa			

Des Moines	41.533	-93.650	1 (pooled)
Cedar Rapids	41.883	-91.700	2
Indiana			
Indianapolis	39.767	-86.150	4
Porter	41.600	-87.067	2
East Chicago	41.633	-87.450	2
Fort Wayne	41.117	-85.117	1
Minnesota			
Minneapolis	44.967	-93.250	1 (pooled)
Finn Church	46.750	-94.933	2 (pooled)
NSP Sherco	45.248	-93.750	2 (pooled)
AS King Plant	44.967	-93.250	1 (pooled)
Ohio			
Columbus	39.950	-82.983	3 (pooled)
Cleveland	41.483	-81.683	2 (pooled)
Kansas			
Topeka	39.033	-95.667	2
Greenland			
South-West Region	67.006**	-50.867**	6

*Natal down used to supplement feather sample

**Eyrie locations averaged in region

Table 3-2. The isotopic delineation of Peregrine Falcon collection areas across study region as determined by Tukey's HSD analyses. Matching combinations of sub-set classifications from Tukey's HSD analyses of hydrogen, carbon and nitrogen stable-isotope ratios were used to differentiate the collection areas (alpha codes). Mean, standard deviation and 95% confidence intervals for natal Peregrine Falcon feathers are provided.

		Tukey's HSD	δD_n‰			$\delta^{13}C$‰			$\delta^{15}N$‰	
Collection Site	**Alpha -code**	**Sub-set (H, C, N)**	***n***	**Mean**	**SD**	***n******	**Mean**	**SD**	**Mean**	**SD**
Porcupine River Region, YK	A	1,a,x	6	-180	2.6	6	-24.0	0.7	8.4	0.8
White River Region, YK	A	1,a,x	4	-178	2.5	4	-23.9	0.6	8.6	0.5
Yukon River Region, YK	A	1,a,x	6	-176	2.4	6	-24.5	0.4	8.8	0.5
MacKenzie River Region, NT	B	2,a,x	9	-155	4.9	9	-23.0	1.7	8.1	1.2
Northern Alaska	B	2,a,x	8	-151	6.3	8	-22.9	0.3	7.6	0.6
Central Alberta	C	2,a,y	10	-145	9.9	10	-23.8	1.2	10.1	1.0
Rankin Inlet, NU	D	2,b,x	10	-123	5.5	10	-20.7	0.2	7.6	0.5
South-Central Alberta	E	3,a,y	11	-116	7.0	11	-22.2	0.9	11.1	0.9

Saskatoon, SK	E	3,a,y	6	-110	10.4	6	-22.8	0.6	10.4	0.5
Regina, SK	E	3,a,y	5	-104	6.0	5	-21.2	1.1	10.3	0.5
Wood Buffalo NP, AB/NT	E	3,a,y	10	-90	14.2	9	-24.2	0.5	10.4	0.9
Winnipeg, MB	F	3,b,y	2	-96	2.0	1	-19.4	-	9.7	-
London, ON	F	3,b,y	9	-95	11.2	9	-19.2	1.1	9.1	0.5
Thunder Bay Region, ON	F	3,b,y	8	-93	8.3	8	-20.4	0.6	9.1	0.2
Toronto Region, ON	F	3,b,y	14	-88	10.4	14	-18.7	1.1	9.3	0.7
Brandon, MB	G	4,a,x	5	-69	39.2	4	-22.8	0.5	7.3	0.2
Quebec, PQ	H	4,a,y	5	-70	4.2	4	-22.1	1.0	9.4	0.7
Minnesota, MN	I	4,b,x	6	-80	7.6	6	-19.0	3.3	8.5	0.6
Ottawa, ON	J	4,b,y	5	-80	10.6	5	-18.2	0.4	9.2	0.4
Iowa	K	4,c,x	3	-78	1.5	3	-17.2	2.6	8.8	0.7
Indiana	K	4,c,x	9	-72	12.6	8	-16.2	1.8	8.6	0.6
Ohio	K	4,c,x	5	-71	15.4	5	-17.8	1.7	8.8	0.7
New Brunswick	L	5,b,x	8	-62	2.8	8	-20.0	1.0	8.9	0.3

Kansas	L	5,b,x	2	-59	2.0	2	-18.4	0.2	8.9	0.3
Greenland	X	6,b,y	6	-15	5.6	6	-19.2	2.2	10.3	1.5
Langara Island, BC	Y	7,c,z	4	48	32.3	4	-15.8	0.5	15.9	0.5
Oregon**	Z	-	1	-41	-	1	-16.9	-	14.3	-

*Carbon and nitrogen are analyzed from the same sample

**The Oregon sample was not included in statistical analyses

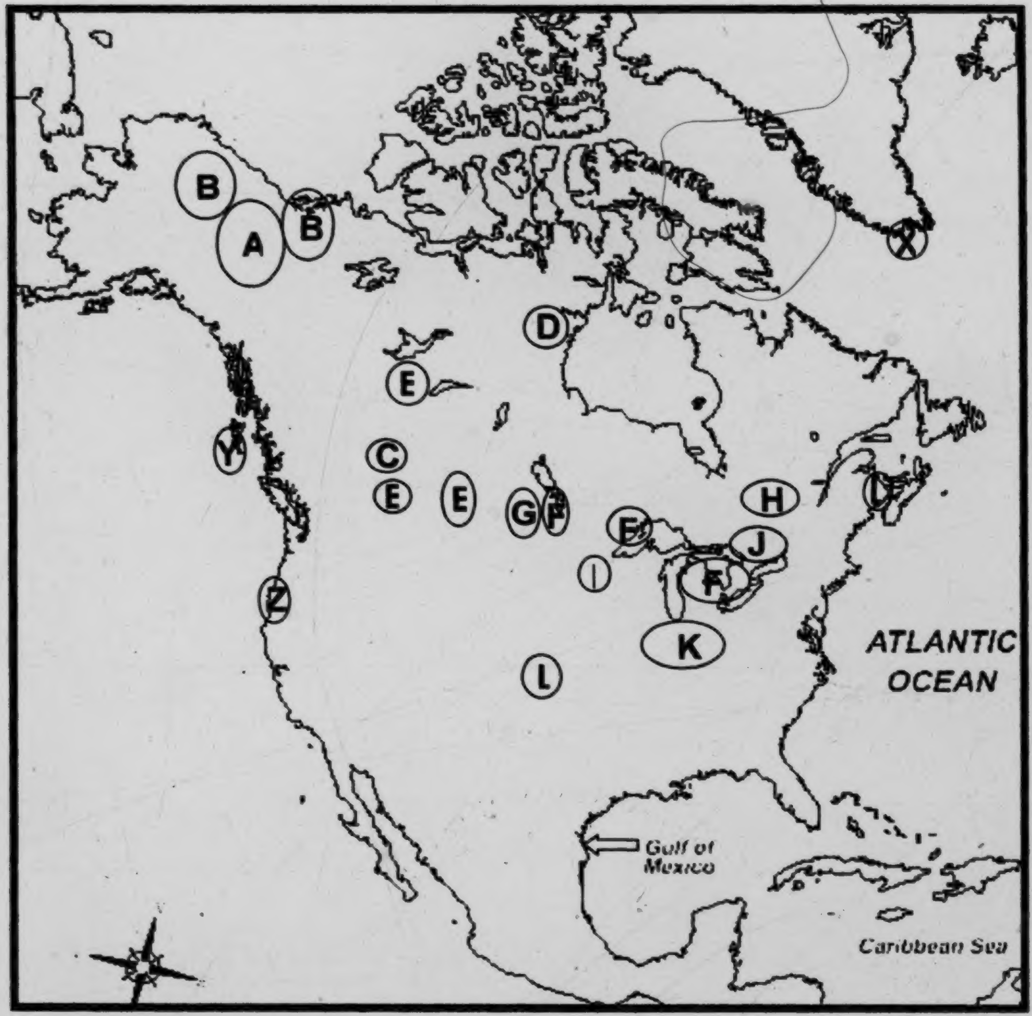

B
A
B
X
D
E
Y
C
E
E
G
F
H
F
J
I
F
Z
K
L
ATLANTIC OCEAN
Gulf of Mexico
Caribbean Sea

Figure 3-1. Feather collection regions of natal Peregrine Falcons as determined by GLM analyses and post-hoc Tukey's HSD tests. Homogenous regions containing multiple collection sites are designated with letters. The arrow indicates the approximate location of the Padre Island migratory falcon banding station.

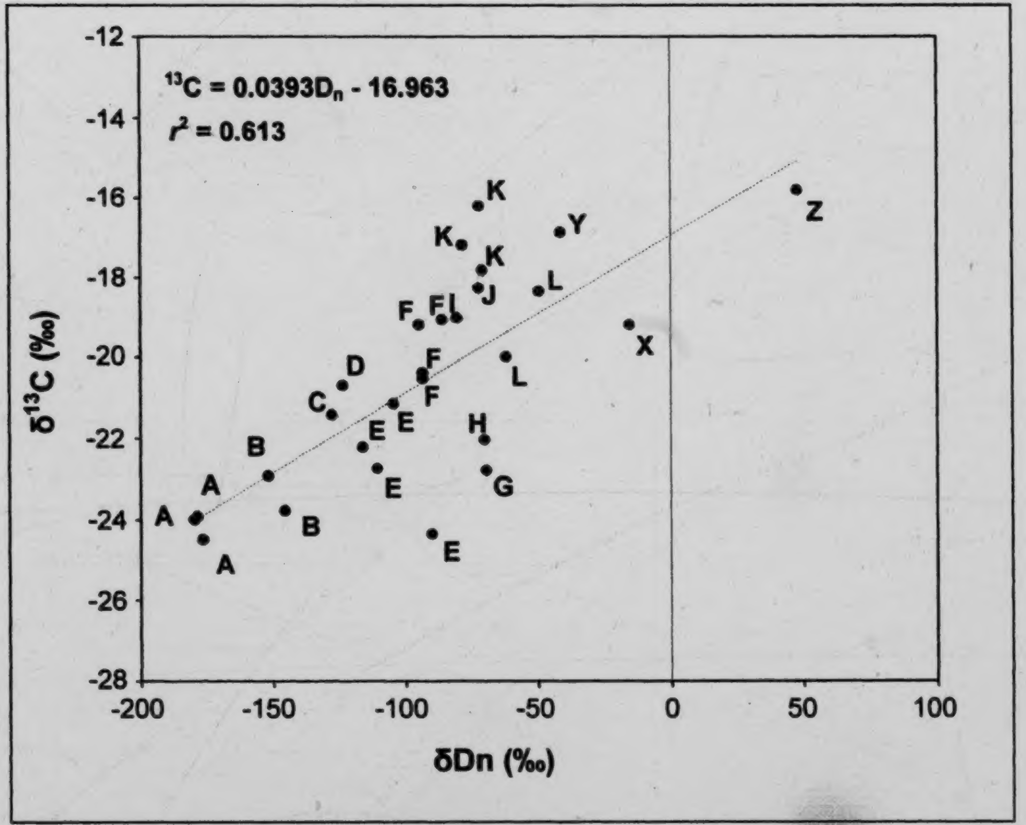


Figure 3-2. The relationship between δD_n and $\delta^{13}C$ values of natal Peregrine Falcon feathers collected across northern North America. Letters refer to collection site categories (Table 3-2). Error bars are ± 1 SD.

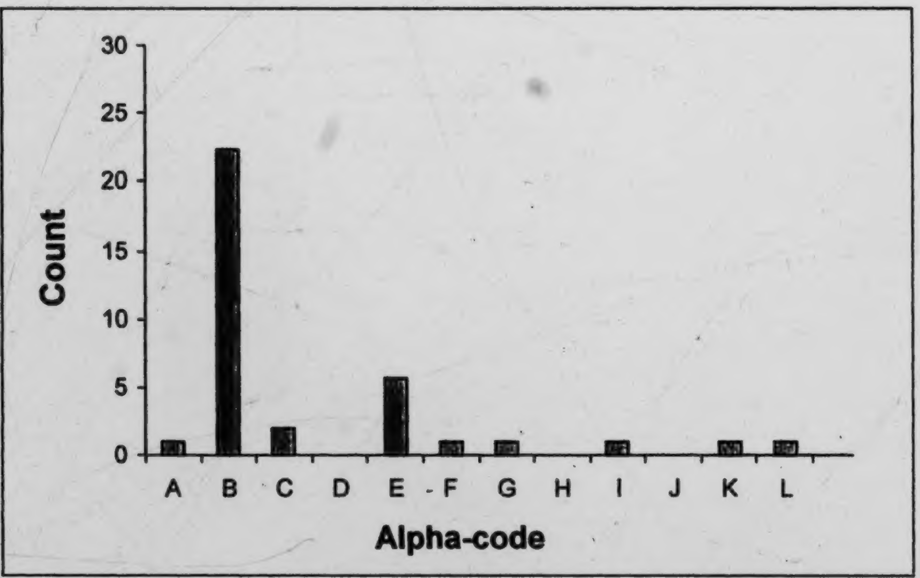


Figure 3-3. Frequency distribution of migrant falcons categorized into regional alpha-codes (see Figure 3-1) based on isotope values of three elements: hydrogen, carbon and nitrogen.

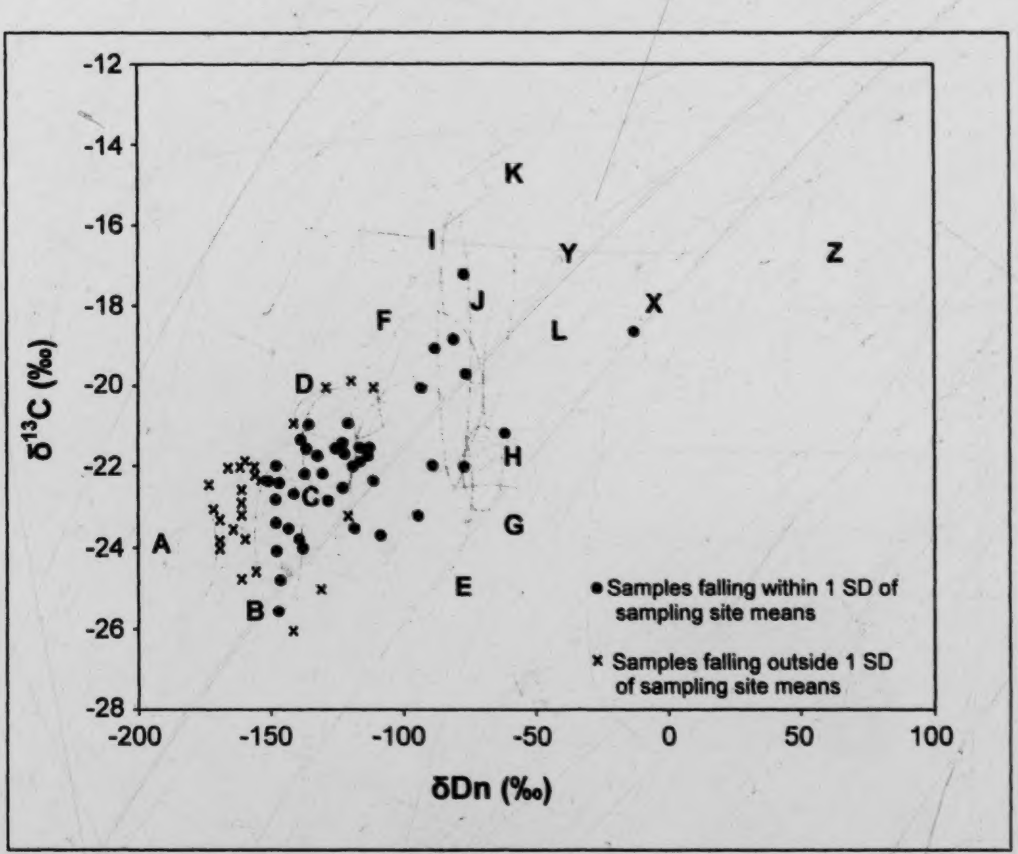


Figure 3-4. Plots of 67 migrant feathers with origins determined by the relationship between δD_n and $\delta^{13}C$ values. Ovals represent areas encircling ± 1 SD of all sample areas within an alpha-code. See Figure 3-1 for alpha-code representation.

LITERATURE CITED

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of Lesser Snow Goose Diets and winter distribution using stable-isotope analysis. *J. Wildl. Manage.* 57:49-54.

Anderson, C.M., D.G. Roseneau, B.J. Walton, and P.J. Bente. 1988. New evidence of a Peregrine migration on the west coast of North America. Pages 507-516 *in* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery.* The Peregrine Fund Inc., Boise, ID USA.

Banasch, U. and G.L. Holroyd. In press. The 1995 Canadian Peregrine Falcon Survey. Occasional Paper. Canadian Wildlife Service, Canada.

Bromely R.G. 1988. Status of Peregine Falcons in the Kitikmeot, Baffin and Keewatin regions, Northwest Territories, 1982-1985. Pages 51-57 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.*], Peregrine Falcon populations: their management and recovery.* The Peregrine Fund Inc., Boise, ID USA.

------ and S.B Matthews. 1988. Status of the Peregrine Falcon in the MacKenzie River Valley, Northwest Territories, 1969-1985. Pages 59-63 *in* T.J. Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery.* The Peregrine Fund Inc., Boise, ID USA.

Caccamise, D.F., L.M. Reed, P.M. Castelli, S. Wainwright, and T.C. Nichols. 2000. Distinguishing migratory and resident Canada Geese using stable-isotope analysis. *J. Wildl. Manage.* 64:1084-1091.

Cade, T.J. and R.W. Fyfe. 1970. The North America Peregrine Falcon survey, 1970. *Can. Field-Nat.* 84:231-245.

Chamberlain, C.P., S. Bensch, X. Feng, S. Åkesson, and T. Andersson. 2000. Stable-isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proc. R. Soc. Lond. B Biol. Sci.* 267:43-48.

------, J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry, and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132-141.

Cherel, Y., K.A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. *Oecologia* 122:155-162.

Cormie, A. B., H. P. Schwarcz, and J. Gray. 1994. Relation between hydrogen isotopic ratios of bone collagen and rain. *Geochim. Cosmochim. Acta* 58:377–391.

COSEWIC, 2000. Canadian species at risk, May 2000. Committee on the Status of Endangered Wildlife in Canada, 23 pp.

Dunn, E.H., D.J.T. Hussell, and R.J. Adams. 1997. Monitoring songbird population change with autumn mist netting. *J. Wildl. Manage.* 61(2): 389-396.

Duxbury, J.M. 1998. An application of stable-isotope ecology to the study of raptor diets. MSc thesis, University of Alberta, Edmonton, Alberta, Canada. 150 pp.

------, G.L. Holroyd, and K. Muehlenbachs. 2003. Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope-base maps for tracking migratory birds. *Isotopes in Environmental and Health Studies* 39:179-189.

Francis, C. M. and D. J. T. Hussell. 1998. Changes in numbers of land birds counted in migration at Long Point Bird Observatory, 1961-1997. *Bird Popul.* 4:37-66.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic composition. *Limnol. Oceanogr.* 33:1182-1190.

Fuller, M.R., W.S. Seegar, and L.S. Schueck. 1998. Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the Western Hemisphere. *J. Avian Biol.* 29:433-440.

Fyfe, R.W., S.A. Temple, and T.J. Cade. 1976. The 1975 North America Peregrine Falcon Survey. *Can. Field-Nat.* 90:228-273.

Graves, G.R., C.S. Romanek, and A.R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proceedings of the National Academy of Science 99:8096-8100.

Hebert, C.E. and L.I. Wassenaar. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environ. Sci. Technol.* 35: 3482-3487

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* 95:7-18.

------ 2002. Science's Compass: Incredible journeys. Science 295:981-982.

------ and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using 13C and 15N analysis. *Mar. Ecol. Prog. Ser.* 84:9-18.

------ and L.I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migration songbirds using stable isotopic analysis of feathers. *Oecologia* 109, 142-148.

------, L.I. Wassenaar, and O.R. Taylor 1999. Stable-isotopes (δD and δ^{13}C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* 120, 397-404.

------, R.B. Brua, W.L. Hohman, and L.I. Wassenaar. 2000. Low frequency of "double molt" of remiges in Ruddy Ducks revealed by stable-isotope: Implications for tracking migratory waterfowl. *Auk* 117:129-135.

------ and L.I. Wassenaar. 2001. Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. *Ecol. Appl.*11:1545-1553.

------, K.P. McFarland, L.I. Wassenaar, C.C. Rimmer, and J.E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable-isotope analyses of feathers. *Auk* 118, 16-23.

Holroyd, G.L. and U. Banasch. 1996. The 1990 Canadian Peregrine Falcon (*Falco peregrinus*) survey. *J. Raptor Res.* 30:145-156.

Holroyd, G.L. and J.M. Duxbury. 1999. Travels of Peregrine Falcon #5735. Blue Jay 57: 146-149.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130:216-221

Kharaka, Y.K. and W.W. Carothers 1980. Oygen and hydrogen isotope geochemistry of deep basin brines. Pages 305-360 *in* P. Fritz and J.C.H. Fontes [Eds.], *Handbook of Environmental Isotope Geochemistry.* Amsterdam.

Kiff, L.F. 1988. Changes in the status of the Peregrine Falcon in North America: an overview. Pages 123-129 *in* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery.* The Peregrine Fund Inc., Boise, ID.

Körner, C., F.D. Farquhar, and S.C.Wong. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia* 88:30-40.

Lajtha, K. and J.D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. Pages 1-21 *in* R.H. Michener and K. Lajtha [Eds.], *Stable-isotopes in ecology and environmental science.* Blackwell, Oxford.

Link, W.A. and J.R. Sauer. 1998. Estimating population change from count data: application to the North American Breeding Bird Survey. *Ecol. Appl.* 8(2) 258-268.

Longmire, J.L. 1988. Identification and development of breeding population-specific DNA polymorphisms within the genome of the Peregrine Falcon. Pages 779-788 *in* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Lott, C.A., T.D. Meehan, and J.A. Heath. 2003. Estimating the latitudinal origins of migratory birds using hydrogen and sulphur isotopes in feathers: influence of marine prey base. *Oecologia* 134:505-510.

Mattox, W.G. and W.S. Seegar. 1988. The Greenland Peregrine Falcon survey, 1972-1985, with emphasis on recent population status. Pages 27-36 *in* T.J Cade, J.H. Enderson, C.G. Thelander, and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Meehan, T.D., C.A. Lott, Z.D. Sharp, R.B. Smith, R.N. Rosenfield, A.C. Stewart, and R.K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. *Condor* 103:11-20.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. *Oecologia* 105:53-63.

Michener, R.H. and D.M.Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. Pages 138-157 *in* R.H. Michener and K. Lajtha [Eds.], *Stable-isotopes in ecology and environmental science*. Blackwell, Oxford.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochim. Cosmochim. Acta* 48:1135-1140.

Morizot, D.C. 1988. Biochemical genetic variability in Peregrine Falcon populations. Pages 773-778 *in* T.J Cade, J.H. Enderson, C.G. Thelander, and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Mossop, D. 1988. Current status of Peregine Falcons in Yukon, Canada. Pages 65-67 *in* T.J. Cade, J.H. Enderson, C.G. Thelander, and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Murphy, J.E. 1990. The 1985-86 Canadian Peregrine Falcon, *Falco peregrinus*, survey. *Can.Field-Nat.* 104:182-192.

Peakall, D.B. 1990. Prospects for the Peregrine Falcon, *Falco peregrinus*, in the nineties. *Can.Field-Nat.* 104:168-173.

Rowell, P., G.L. Holroyd, and U. Banasch. 2003. The 2000 Canadian Peregrine Falcon Survey. *J. Raptor Res.* 37:98-116.

Rubenstein, D.R., C.P. Chamberlain, R.T. Holmes, M.P. Ayres, J.R. Waldbauer, G.R. Graves, and N.C.Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. *Science* 295:1062-1065.

Shearer, G., D.H. Kohl, and S.-H. Chien. 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America Journal 42:899-902.

Schimmelmann, A. 1991. Determination of the concentration and stable isotopic composition of nonexchangeable hydrogen in organic matter. *Anal. Chem.* 63:2356-2459.

Schulze, E.D., F.S. Chapin, III, and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* 100:406-412.

Sheppard, S.M.F. 1986. Characterization and isotopic variations in natural waters. Pages165-177 *in* J.W. Valley, H.P. Taylor, and J.R. O'Neil [Eds.], *Reviews in Mineralogy Vol. 16:Stable-isotopes in High Temperature Geological Processes*. Mineralogical Society of America, BookCrafters Inc., Chelsea, MI

USDI (United States Department of the Interior). 1994. Endangered and Threatened Wildlife and Plants; final rule to remove the American Peregrine Falcon from the federal List of endangered and threatened wildlife. *Federal Register* 59: 50796-50805.

------ 1999. Endangered and Threatened Wildlife and Plants; final rule to remove the American Peregrine Falcon from the federal List of endangered and threatened wildlife. *Federal Register* 164: 46542-46558.

USGS. (United States Geological Survey). 2003. Non-Game Banding Records 1955 – 2002. http://www.pwrc.usgs.gov/pubdata/pubdata.htm.

Van der Merwe, N.J., J.A. Lee-Throp, J.F. Thackeray, A. Hall-Martin, F.J. Kruger, H. Coetzee, R.H. Bell, and M. Lindeque. 1990. Source-area determination of elephant ivory by isotopic analysis. Nature 346:744-746.

Vogel, J.C., B. Eglinton, and J.M. Auret. 1990. Isotope fingerprints in elephant bond and ivory. Nature 346:747-749.

Ward, F.P., K. Titus, W.S. Seegar, M.A. Yates, and M.R. Fuller. 1988. Autumn migrations of Peregrine Falcons at Assateague Island, Maryland / Virginia, 1970-1984. Pages 485-495 *in* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Wassenaar, L.I. and K.A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. *Proc. Natl. Acad. Sci. USA* 95: 15436-15439.

------ and K.A. Hobson. 2000. Evaluating the use of stable-carbon (δ^{13}C) and H (δD) isotope ratios in feathers to infer breeding origins of Red-winged Blackbirds. *Ecol. Appl.* 10:911-916.

------ and K.A. Hobson 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environ. Sci. Technol.* 35:1845-1850.

White, CM, RW Fyfe, and DB Lemon. 1990. The 1980 North American Peregrine Falcon, *Falco peregrinus*, survey. *Can. Field-Nat.* 104:175-181.

Yates, M.A., K.E. Riddle, and F.P. Ward. 1988. Recoveries of Peregrine Falcons migrating through the eastern and central United States, 1955-1985. Pages 471-483 *in* T.J Cade, J.H. Enderson, C.G. Thelander and C.M White [Eds.], *Peregrine Falcon populations: their management and recovery*. The Peregrine Fund Inc., Boise, ID.

Chapter 4

Summer origins of Burrowing Owls wintering in Southern Texas and Central Mexico as determined by stable-isotope analysis[3]

The Burrrowing Owl (*Athene cunicularia hypugaea*) is an Endangered Species that is annually declining by over 20% in Canada (Wellicome and Haug 1995, Skeel et al. 2001, Wellicome and Holroyd 2001). The species was extirpated from the provinces of British Columbia and Manitoba (Wellicome and Holroyd 2001). Limiting factors in the summer such as low productivity, predation, and road kills are contributing to the decline of Burrowing Owl populations (Schmutz 1997, Poulin et al. 1999, Wellicome 2000, King and Beltoff 2001, Poulin et al. 2001, Sissons et al. 2001, Todd 2001). A low recruitment rate into Canadian populations is another possible cause of the decline of the owls, and is a key concern in the conservation plan derived at the second international Burrowing Owl symposium in Ogden, Utah in 1998 (Holroyd et al. 2001).

Over-winter mortality may be an important factor contributing to the low recruitment of new owls to populations in Canada (Poulin et al. 1999). To study the causes of over-winter mortality, the location of owls in the winter must be determined. The link between Burrowing Owls found in Mexico and the southern US in the winter and their potential breeding populations in Canada is far from being completely understood (Holroyd et al. 2001). Little has been published regarding the status of migratory Burrowing Owls wintering in Mexico. The small amount of information that exists is primarily focused on distribution rather than ecology (Holroyd et al. 2001). Knowledge of winter destinations and distribution of Burrowing Owls is crucial for better understanding the connectivity between the owls' seasonal ecological requirements, and ultimately the relative importance of seasonal mortality on recruitment.

---

[3] *This chapter has been formatted for submission to the Auk.*

Until recently, the technique to determine the breeding season origin of wintering owls was limited to the recovery of leg bands. However, band recoveries are a rare event. Of the 19,027 Burrowing Owls banded in North America, only 272 (1.4%) have ever been recovered (USGS 2003a). The most southerly band recoveries of owls that hatched or bred in Canada have been southern Texas and Louisiana and they were recovered in the spring and autumn. However, a long term, ambitious search for owls was rewarded in 2001 with six relocations of owls that had carried radio-transmitters to southern Texas and central Mexico from Alberta and Saskatchewan (G. Holroyd unpubl. data). One relocation in Mexico was in a relatively large winter population of Burrowing Owls in the Bahio Mexicano ecoregion of central Mexico (G. Holroyd unpubl. data). Except for the owl located by radio-transmitter, the summer origins of the other Burrowing Owls in this region could not be discerned. Without radio-transmitters or bands, conventional migration tracking methodologies cannot determine the summer origins of the owls.

The study of migratory animals using stable-isotope analyses (SIA) provides a relatively new method to estimate the natal/breeding origins of wintering Burrowing Owl without dependence on leg bands. Hydrogen isotope ratios (δD) in precipitation exist in predictable patterns across North America. Chamberlain et al. (1997) and Hobson and Wassenaar (1997) were first to demonstrate that the hydrogen isotope ratios are passed up food chains to create correlated continental patterns in the feathers of birds. Carbon (^{13}C) and nitrogen (^{15}N) isotope ratios also exist in various patterns dependent upon physiological processes of different ecosystems, elemental sources, and climate (Van der Merwe et al. 1990, Vogel et al. 1990, Körner et al. 1991, Schulze et al. 1994, Lajtha and Marshall 1994, Michelsen et al. 1996, Chamberlain et al. 1997, Chamberlain et al. 2000, Hobson and Wassenaar 2001, Graves et al. 2002, Rubenstein et al. 2002). Enrichment of ^{15}N levels has also been associated with agriculture and can create differences in nitrogen isotope ratios between adjacent regions exposed to the same climate conditions (Duxbury 1998, Hebert and Wassenaar 2001). Stable-isotope ratios of carbon and nitrogen are also altered depending upon how many trophic levels exist below the study species (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1992, Hobson 1993). The above-mentioned causes of stable-isotope ratio variation produce large-scale, continental patterns that can be ultimately detected in animal tissues through SIA (Hobson 2002).

The delineation of regions of breeding Burrowing Owls and back-tracking of migrants has been made possible by taking advantage of these continental patterns in stable-isotopes (Alisauskas and Hobson 1993, Chamberlain et al. 1997, Hobson and Wassenaar 1997, Caccamise et al. 2000, Chamberlain et al. 2000, Hobson and Wassenaar 2001, Wassenaar and Hobson 2001, Kelly et al. 2002, Rubenstein et al. 2002). The most accurate method for isotope tracking is comprised of two steps. The first step is the creation of a stable-isotope database from con-specific nestlings. The second step is the determination of the isotopic signatures of migrants or wintering birds. The isotopic signatures are then compared to the nestling dataset (Wassenaar and Hobson 1998, Hobson et al. 1999, Cherel et al. 2000, Hobson et al. 2000, Hebert and Wassenaar 2001, Hobson and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001).

Before the origin of wintering owls can be determined through SIA, the areas where the owls may have grown their feathers must first be described "isotopically" (Wassenaar and Hobson 2000, Hebert and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001). The evolution of this technique has led to increased accuracy in estimating the origins of migrants by sampling young-of-the-year throughout the breeding range of a species (Wassenaar and Hobson 2000, Hebert and Wassenaar 2001, Hobson and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001). The greatest accuracy in delineating the origins of migrants has been demonstrated by studies that were able to obtain samples from the majority of the breeding range (Wassenaar and Hobson 1998, Hobson et al. 1999, Hobson et al. 2001). The determination of the regional differences in isotopic signatures throughout the whole range, without heavy dependence on model interpolations, increases the accuracy of extrapolations of areas not sampled for the creation of the reference dataset. Therefore, the collection of samples from young-of-the-year from the greatest proportion of the breeding range is important for the accurate tracking of migratory animals.

The second component of stable-isotope tracking is the analysis of tissues collected from migrants after they depart from their breeding grounds. Migrants caught along their migration routes or on their wintering grounds can be sampled for tissues grown on their natal / breeding grounds. The isotope values of the migrants' tissues are associated with potential natal / breeding areas that have similar isotope values (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 1999, Chamberlain et al. 2000, Cherel et al. 2000, Hobson et al. 2000, Hebert and Wassenaar 2001, Hobson and Wassenaar 2001, Hobson et al. 2001, Meehan et al. 2001, Rubenstein et al. 2002). The relative proportion of migrants originating from different parts of their range can then be determined without the dependence on band returns and transmitter relocations. SIA was used to determine the summer origins of Burrowing Owls wintering in central Mexico, Texas and New Mexico.

METHODS

FEATHERS FOR REFERENCE DATASET

Researchers conducting field studies across the range of the western Burrowing Owl collected feathers for this project (Table 4-1, Fig. 4-1). Many Burrowing Owl studies included nest visits and feathers could be collected from nestlings when they were being banded. For the creation of the isotope reference dataset, the samples were either juvenile down, juvenile body feathers or the tip of a tail feather. The feather collection continued from 1997 until 2003. Natal feathers were obtained from the prairie provinces of Alberta and Saskatchewan in Canada, and from 12 states of the United States of America. Many provinces and states had multiple collection sites. The sample size obtained from each region was reflective of the amount of research being conducted on the various collection areas. Museum collections were occasionally used to augment the sample collection.

This is the first stable-isotope / migration study to require the isotopic profile for central Mexico as some of the owls encountered in the winter may be short-distance migrants. To obtain an estimate of the isotopic signature of the area where the winter samples are obtained, feathers of Barn Owls (*Tyto alba*) and feral urban pigeons (*Columba livia*) were analyzed. It should be noted that while the majority of the North American Barn Owl population is thought to be non-migratory (Marti 1992), the migratory status of those sampled in Mexico was unknown.

FEATHERS FROM WINTERING BURROWING OWLS

The collection of feathers from Burrowing Owls on their wintering grounds began during the winter of 1998/1999 and continued every winter until January 2003. A large proportion of winter samples were moulted body feathers found near roosts. When possible, owls were trapped and a sample of a tail feather was collected along with a body feather. A primary or tail feather was collected from the remains of dead owls. Winter samples were obtained from the states of New Mexico and Texas in the US; and Aguascalientes, Chihuahua, Durango, Guanajuato, Jalisco, Sonora, Tamaulipas, and Zacatecas in Mexico (Fig. 4-1).

TESTS OF CONFIDENCE

A test was conducted to establish confidence in the isotope tracking process. Feathers were obtained from two wintering Burrowing Owls located by radio-telemetry and a band recovery. These feathers were analysed to see if their isotope values matched the parameters of the population from which they originated. The samples were analyzed blindly to control analytical bias.

FEATHER ANALYSES

Feathers were washed with a mild solution of detergent and water. Surface oils were removed with a 2:1 solution of chloroform and methanol. Feathers washed with the solution were allowed to dry in a fume hood before they were sampled and weighed. Between 7-10 mg of feather tissue were required for offline hydrogen analyses, and 1 mg was required for the online carbon and nitrogen analyses.

Hydrogen. - Feathers are almost completely composed of keratin protein. Most of the hydrogen in keratin is inertly bonded to carbon atoms. However, hydrogen atoms are also weakly bonded to the nitrogen and oxygen atoms of the protein molecules. The weak bonds can lead to exchange with hydrogen in ambient water vapour (Schimmelmann 1991). This exchange can introduce erroneous results associated with storing samples away from the collection site.

To control the effects of the exchangeability of hydrogen, samples were equilibrated under controlled conditions using a modified method similar to those developed by Schimmelmann (1991) and Wassenaar and Hobson (2000). With the use a steam chamber, the samples were exposed to water vapor with a hydrogen isotopic value of -146‰ at 130°± 0.1C for a period of two hours. The samples were then allowed to slowly return to room temperature. Samples were sealed under vacuum and combusted at 850°C for another two hours, and were gradually allowed to return to room temperature. The resulting water vapor was reduced to H_2 gas over hot zinc. Hydrogen from the feather samples was analyzed with the use of a duel-inlet, Finnigan-MAT 252 mass spectrometer. Hydrogen isotopic values are reported as δD values and are in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. Results were normalized using VSMOW/GISP/SLAP scale. Water samples analyzed with each batch of feathers produced a 95% confidence interval of ± 1‰ (n=54). An isotopic fractionation factor of +80‰ was used in calculating the δD values of the non-exchangeable hydrogen (D_n)(equation 2, Hobson et al. 2001). Samples were equilibrated and analyzed randomly in order to minimize the introduction of temporal and isolation biases (Hurlbert 1994).

Carbon and Nitrogen. - One mg of a feather sample was placed in a tin cup and combusted in a Robo-Prep elemental analyzer at 1800°C. The resultant CO_2 and N_2 were analyzed with the use of an inter-faced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS). Carbon isotope ratios ($\delta^{13}C$) are expressed relative to the PeeDee Belemite (PDB) international standard. Nitrogen isotopic ratios ($\delta^{15}N$) are expressed relative to atmospheric N_2. Analytical error was measured at ± 0.1‰ and ± 0.3‰ for stable-carbon and nitrogen isotope measurements respectively.

DATA ANALYSIS

Feathers were grouped by body and flight feathers. Burrowing Owls undergo a complete flight feather moult on their breeding grounds (Haug et al. 1993), and no owls were found moulting flight feathers on the wintering grounds (G. Holroyd pers. obs.). Therefore, the isotopes of flight feathers should be indicative of where a wintering owl bred or was raised the preceding summer. While more moulted body feathers were found on the wintering grounds, they were also found at nests and roosts in the summer. The moult pattern of various body feather tracts has not been described and the origin of the body feathers may not be indicative of the winter grounds. Without knowledge of the consistency of body feather moult, body feathers cannot provide a direct link between the summer and winter grounds. However, an estimation of where body feathers are grown is still of interest. Therefore, flight and body feathers were kept separate for analyses (except for the New Mexico collection where only 5 samples were collected in total).

A multivariate General Linear Model procedure (GLM) was used to determine if significant variability existed among the isotopic values of the natal feathers across the geographic range of the study. The samples were categorized by collection areas. Each element (H, C, N) was analyzed separately and grouped into homogenous sub-sets of isotopic values by a post-hoc Tukey's HSD (α=0.05). Unique combinations of sub-sets from the three Tukey's HSD analyses were used to differentiate the collection areas. To determine if a linear relationship existed between hydrogen and carbon isotope values in the natal feathers, a regression was conducted with δD_n values against $\delta^{13}C$ values. A linear regression was also used to determine if there was a relationship between δD_n values and latitude, and $\delta^{15}N$ values and latitude. Once the isotope dataset was created, the origins of wintering Burrowing Owls were estimated by a comparison of the isotope values of the feathers from the wintering owls to the parameters of the isotopically delineated collection areas. Wilcoxon-signed rank tests were used to make comparisons between wintering collection areas and between flight and body feathers analyses. Statistical analyses were conducted using SPSS v.11.

RESULTS

ISOTOPE REFERENCE DATA-SET

A total of 161 feathers from natal Burrowing Owls from 19 collection areas were analyzed to create an isotope reference dataset (Table 4-1). Ten samples (6.5%) of juvenile down were used in the creation of the dataset, but the remainder of the samples (93.5%) were from nestling juvenile plumage (body feathers, or small samples from flight feathers).

Mean isotope values of collection areas varied significantly across the range of the Burrowing Owl (GLM *Pillai's Trace* $F_{57,309} = 27.0$, $P<0.0001$). The mean δD_n values ranged from -115‰ to -56‰ (GLM $F_{19,133} = 45.53$, $P<0.0001$; Table 4-2). Collection areas located in the southern portion of the range, generally had relatively enriched δD_n values, while more northerly regions had relatively more depleted δD_n values. The omega pattern of continental δD values in meteoric water predict that areas west of the Rocky Mountains will have similar δD values as other areas east of the mountains (Kharaka and Carothers 1980, Sheppard 1986, Hobson and Wassenaar 1997). The omega pattern is due to the fractionation effects correlated to changes in altitude (Kharaka and Carothers 1980, Sheppard 1986, Hobson and Wassenaar 1997). This pattern was reflected in the hydrogen isotope reference dataset based on the owl nestlings. The collection sites of west coast states were found to have similar δD_n values of those of the northern Great Plains (Fig. 4-1). However, as Kelly (2002) documented, there was still a strong relationship between δD_n values and latitude ($F_{1,13}$ = 14.19, P < 0.002, r^2 = 0.565; Fig. 4-2). The expected depletion between δD values of precipitation and the non-exchangeable D of feathers (Cormie *et al.* 1994, Wassenaar and Hobson 2001) ranged from approximately 20-30‰ depending on the location of the sample collection site.

Differences in collection site mean δ^{13}C values across the study area was also significant (-24.6 to -17.2‰)(GLM $F_{19,103}$ = 45.22, P<0.0001). As with the δD_n values, the δ^{13}C values also fell into a gradient with relatively more depleted values associated with the northern regions (Table 4-2). A significant relationship was found between the δD_n and δ^{13}C values across the continental range of the study ($F_{1,19}$ = 42.64, P < 0.0001, r^2 = 0.654; Fig. 4-3).

The mean δ^{15}N values significantly differed between collection areas (GLM, $F_{19,103}$ = 19.00, P<0.0001). A relationship between δ^{15}N values and latitude was theoretically possible because feather collections were made in the arid south west of the US (Shearer et al. 1978 and 1983). Nonetheless, a relationship between the δ^{15}N values of natal Burrowing Owls and latitude was not significant ($F_{1,19}$ = 2.00, P = 0.176, r^2 = 0.111; Fig. 4-3). However, 4 of 19 collection areas (21.1%) were separable by only their δ^{15}N values in the Tukey's HSD analysis.

The Tukey's HSD test grouped the δD_n, δ^{13}C and δ^{15}N values into 7, 4 and 4 homogenous sub-sets respectively (Table 4-2). A decrease in the number of sub-sets indicated a decrease in variability in the isotope values across the study range. The three sets of Tukey's classifications were then combined for each region. Regions with the same combination of Tukey's classifications were categorized into groups lettered A-Q (Table 4-2, Fig. 4-1). The alpha-coding process included data from the Barn Owls and feral pigeons collected in Mexico. The feathers from the Barn Owls and feral pigeons from the same area had similar δD_n values (Barn Owls x=- 59, n=2; pigeon x=-61, n=5). Only the $\delta^{13}C$ and $\delta^{15}N$ values from the Barn Owl analyses were used for the reference data due to potentially large differences in diet between the owls and pigeons.

MIGRANT TRACKING

The blind test of a feather from each of the radio-tagged and banded owls was supported the theory of isotope tracking. The isotopic values of all three elements in both feathers fell within the parameters of the area where the owls were originally captured on the Regina Plain, SK (Table 4-3).

One hundred and sixty-nine feather samples that were collected between 1998 and 2003 from wintering Burrowing Owls in Mexico, Texas and New Mexico were analyzed (Table 4-4). The wintering owl isotope values were placed into the same alpha-code categories used in the creation of the reference dataset. The summer origins were estimated for 94 samples (55.6%) with isotopic values that did not fall within the ranges of δD_n, $\delta^{13}C$ and $\delta^{15}N$ values of the collection areas. Origin estimation was based on the relationships between δD_n and $\delta^{13}C$

values and δD_n values and latitude as found in this study. The established relationship between δD values in feathers and precipitation (Hobson and Wassenaar 1997, Wassenaar and Hobson 2001) was also used as a guide.

Both Texas and Mexico had samples with origins in Canada or the northern US (Fig. 4-4). However, the Mexican sample collection contained relatively more flight feathers that originated from southerly locations (Wilcoxon, $z=2.15$, $p<0.05$). In general, the δD_n values of all feathers from wintering Burrowing Owls were skewed towards relatively enriched values (Fig. 4-4). Of the 43 flight feather samples collected in Mexico, 18 (41.9%) had values more enriched than any feather used to create the reference dataset. Thirty-seven of 88 (42.0%) body feathers in central Mexico had δD_n values more enriched than values in the reference dataset (Fig. 4-4). In the Texas collection, six of 20 (30%) flight feathers and seven of 13 (53.8%) body feathers had very enriched δD_n values. Two of the four feathers collected in New Mexico had relatively enriched δD_n values and two had δD_n values that associated them with locations north of the winter collection site.

Comparisons between flight and body feathers of the same owls indicated that body feathers were more enriched than the flight feathers (paired t-test, $t=-2.8$, $n=13$, $P<0.02$ (Fig. 4-5). Overall, the distribution of the origins for body and flight feathers collected in Mexico were significantly different (Wilcoxon, $z=2.62$, $p<0.01$)(Fig. 4-4). Although more flight feathers than body feathers originated from northern locations, the distribution of the origins of feathers collected in Texas were not statistically separable (Wilcoxon, z=0.91, p=0.36) (Fig. 4-4).

Long Distance Migrants. - In addition to the feather collected from the radio-tagged owl in Mexico, three flight and three body feathers collected in the winter in Mexico had isotopic values that matched all three of the parameters of regions in the northern-most section of the breeding range (Table 4-3, Fig. 4-4). One flight feather was linked to the most northern area of the Burrowing Owl range in Alberta, the second to the Regina Plain of southern Saskatchewan, and the third to the Fort Belknap I.R. of northwest Montana or to southeast Washington. Two body feathers could be linked to Saskatchewan, one with isotope values matching Grasslands National Park and the other matching those of the Regina Plain. The third body feather was from either Montana or Washington State. Within Mexico, some wintering areas (Guanajuato) contained long distant migrants while others did not (Jalisco). For example, of the 69 analyzed samples from Guanajuato, five originated as far north as the Canadian / US border. Of the 30 samples from Jalisco, the most northern origin appeared to have been Kansas west to southern California (Figs. 4-1 and 4-6). The difference in origin distributions between collection areas was statistically significant (Wilcoxon, z=2.9, p<0.01).

In addition to the band recovery in Texas, another feather had isotope values that fell within the three parameters of an area of Canada (Table 4-3).

The isotopic values of a feather collected near Corpus Christi matched those of of southern Alberta. Three other flight feathers collected in Texas had relatively depleted δD_n values. The origin of these feathers is estimated to be from a large region between southeast Washington State, western North Dakota and eastern Wyoming (Table 4-3).

DISCUSSION

Most of the collection areas for western Burrowing Owl samples in this study were separable by stable-isotope values of hydrogen, carbon and nitrogen. The pattern in δD_n values of collection areas across North America was similar to those predicted or measured by previous studies of other species (Wassenaar and Hobson 2001, Kelly et al. 2002). A significant continental gradient was detected in both hydrogen and carbon isotopes ranging from southern New Mexico to southern Alberta. A gradient in $\delta^{13}C$ values across the range of a species has not always been detected when delineating regions by isotopes (Hobson et al. 2001, Wassenaar and Hobson 2001, Graves et al. 2002). However, the continental gradient of this study supports other previous studies that found latitudinal patterns in carbon isotope ratios (Chamberlain et al. 1997, Wassenaar and Hobson 1998, Hobson et al. 1999, Hobson and Wassenaar 2001, Rubenstein et al. 2002). The latitudinal gradient in $\delta^{13}C$ values of this Burrowing Owl study may have been detectable due to the lack of acute changes in altitude within the sampling range (Graves et al. 2002).

There was no expectation of a continental gradient for $\delta^{15}N$ values. A distinct pattern was not detected, but differences in mean $\delta^{15}N$ values allowed for the occasional distinguishing of adjacent collection areas. Some of the regions with relatively more enriched $\delta^{15}N$ values are associated with areas that include intensive agriculture practices (eg. Regina Plain, SK and the Salton Sea area of the Imperial Valley of southern California). These results are consistent with other comparisons of $\delta^{15}N$ between samples from areas where there is minimal or intensive agriculture but exist in similar climatic conditions (Duxbury 1998, Hebert and Wassenaar 2001).

Most of the Burrowing Owls wintering in central Mexico appear to be short-distant migrants (Figs. 4-1 and 4-4). The distribution plots of flight feathers indicate that the majority of the wintering migrants originated in an area that includes the southern US and possibly northern Mexico (Fig. 4-4). Only a standardized continental survey will determine whether or not the high number of wintering owls from the southern half of their breeding range is reflective of relative regional densities. Another possibility is that the central Mexico area is the destination for short-distance migrants and the majority of long-distant migrants are flying further south. Very few Burrowing Owls are recorded in the US during winter surveys (CBCs; USGS 2003b). Therefore it is unlikely that owls from the northern portion of their range are remaining in the US during the winter. The determination of a possible "leap-frog" migration will require the samples from more southern Burrowing Owl wintering grounds.

While the isotopic values of the body and flight feathers had a similarly skewed distribution, the body feathers had more values that are indicative of feathers grown during the winter (Fig. 4-4). Of the body feather samples from Mexico, 18.2% had values possibly reflecting the wintering grounds. In comparison, the proportion of flight feathers was only 7%. Thirteen owls were sampled for both flight and body feathers. On average, body feathers of wintering owls were 12‰ more enriched than the flight feathers indicating that most body feathers were grown at a more southern location (Fig. 4-5). It may also be possible that feathers are lost and replaced during migration and produce an intermediate isotope value. Some body feathers may be useful to track wintering owls, but without a better understanding of the seasonal moulting patterns of Burrowing Owls, results from flight and body feathers should not be analyzed together (but see Kelly et al. 2002). Therefore, flight feathers are the feathers to sample for the determination of summer origins.

In addition to the band recovery and the radio-transmitter relocations, SIA has established another five links between Mexico and Canada. Two other feathers had values consistent with regions adjacent to the Canadian border. These results provide supplemental support that central Mexico is a winter destination for some Burrowing Owls breeding in Canada. However, only some of the collection areas in Mexico contained owls that likely bred in the northern edge of their range (Figure 4-6). Five feathers collected Guanajuato were estimated to originate in the northern Great Plains, but none of the feathers collected in Jalisco were linked to northern breeding grounds (Figure 4-1, 4-6). The SIA results also added another link between the Texan wintering area and Canada, with three other samples matching northern US collection areas. Band recoveries and the SIA results suggest that southern Texas is also used by wintering "Canadian" owls.

Until recently, information regarding the wintering location of Burrowing Owls breeding in Canada was non-existent. Little more is known about Burrowing Owl winter ecology (Holroyd et al. 2001). The breeding/natal origins of most owls wintering in central Mexico and southern Texas have yet to be determined. The method of delineating regions by stable-isotope analysis has provided new information about Burrowing Owl migratory patterns. Band recoveries indicate two possible migration routes; southwest from areas west of the continental divide, and southeast from areas east of the divide (Haug et al 1993). Band recoveries of Burrowing Owls banded in Idaho suggest owls west of the continental divide may migrate to wintering grounds in California (King and Belthoff 2001). Band recoveries from owls banded in the Great Plains indicate wintering grounds in southern New Mexico and Texas, as well as, northern and central Mexico (Haug et al. 1993). The SIA results indicate that Burrowing Owls from Washington State and California may find their way to Mexico for the winter. Such migratory pathways would involve crossing the continental divide. The ability of Burrowing Owls to cross the continental divide has been demonstrated by the recent event of an owl banded in Arizona and subsequently recaptured in Saskatchewan only 2 months later (G. Holroyd and C. Conway unpubl. data).

The results of this study are an important step towards the development of a continental approach to conserving Burrowing Owls as called for by the Canada/Mexico/United States Trilateral Committee for Wildlife and Ecosystem Conservation and Management in 1997. The creation of links between winter grounds and breeding populations should lead to multi-lateral conservation efforts between organizations in Canada, the US and/or Mexico.

FUTURE RESEARCH

Comprehensive sampling of breeding populations needs to continue. Some regions require additional collections for greater definition. Many other areas have yet to be sampled. It should be noted that many of the links to breeding locations made in this study should not be considered exact. Without complete coverage of all breeding populations, the isotopic signatures of adjacent regions are unknown and may be similar to the areas that were sampled. For example, the combination of isotope values to establish links between California and Mexico included δD_n values that are within the parameters of the North Dakota / Wyoming subset. However, the carbon and nitrogen values match California population parameters. It is possible that there are other regions in North Dakota or Wyoming with matching $\delta^{13}C$ and $\delta^{15}N$ values. Such a determination would be significant to the overall pattern of inter-regional dynamics.

Survival estimates of Burrowing Owls based on band recoveries indicate they may not live much more than four years in the wild (although an owl has lived to eight years)(Haug et al. 1993). For an owl with a short life span, both summer and winter philopatry may be secondary to settling at the first detection of suitable habitat, space and resources. As well, interactions with mates during the winter as with some waterfowl species is not known to occur, reducing the requirement to return to the same winter location each year (Cooke et al. 2000). Yearly, repeated sampling in known wintering grounds will help establish whether the mean isotope values shift between years. Annual shifts in mean isotope values would indicate the proportion owls from different summer grounds is changing.

Winter sampling from areas in the southern US that in the summer are comprised of migrant and resident Burrowing Owls also needs to be conducted. It may be possible to determine the relative proportion of migrants and residents in these areas and the origin of the migrants. Finally, since some body feathers may reflect winter isotopic signatures, the establishment of migratory links may be feasible by collecting certain feathers from owls that arrive in the spring.

ACKNOWLEDGEMENTS

I would like to thank L. Priestley, and D. Birn for their assistance in the lab. Many thanks go to the feather collectors because without them, this study would not have been possible: G. Holroyd, H. Trefry, D. Shyry, R. Sissons, D. Scobie, R. Russell, J. Nicholson, D. Todd, R. Poulin, P. Bartels, J. Belthoff, R. Griebel, D. Rosenberg, L. Trulio, J. Barclay, P. Delevoryas, G. Proudfoot, G. Batey, N. Korfanta, E. Valdez, C. Conway, J. Everett, M. Robbins, J. Sleno, P. Arrowood, and M.K. Skoruppa. Also, thanks to Environment Canada's Stable-isotope Laboratory for running the C&N analyses. I am grateful to H. Trefry for completing the permit application process, and MK. Skoruppa for organizing and shipping feathers from the US. Special thanks go to G. Holroyd of the Canadian Wildlife Service for his endless logistical and financial support. Special thanks also go to K. Muehlenbachs of the Department of Earth and Atmospheric Sciences at the University of Alberta for his guidance in stable-isotope analysis, and for providing laboratory space and in-kind support. Approval for this project was provided by the Animal Care Committee of the Canadian Wildlife Service. Finally, I am grateful to Environment Canada; the Natural Sciences and Engineering Research Council of Canada; Alberta Sports, Recreation, Parks, and Wildlife Fund; National Fish and Wildlife Foundation (US); and the University of Alberta for funding this project.

Table 4-1. Collection sites for nestling Burrowing Owl feather samples. Latitude and longitude represent the mean of all sites in the region.

Site	Latitude	Longitude	*n*
Alberta			
Hanna Region	51.26	-111.66	18
Eastern Irrigation District	50.21	-111.37	20
Saskatchewan			
Grasslands National Park	49.16	-105.04	12
Regina Plain Region	49.75	-102.30	6
Arizona			
Tucson region	32.27	-110.58	10
California			
Salton Sea	33.25	-115.95	7
Carrizo Plain	35.18	-119.78	5
Lamoore NAS	36.30	-119.77	3
San Jose Aiport	37.30	-121.92	10
Santa Clara / Alamede Counties	37.40	-122.10	10

Kansas			
Western region	38.97	-95.23	3
Montana			
Fort Belknap I.R.	48.20	-108.53	6
Nevada			
South-east region	36.31	-115.28	3
New Mexico			
Las Cruces region	32.30	-106.77	11
North Dakota			
Little Missouri National Grassland	47.00	-103.50	6
South Dakota			
Buffalo Gap National Grassland	43.58	-102.16	7
Texas			
Lubbock	33.67	-101.82	6
Washington			
South-east counties	46.23	-119.04	10
Wyoming			
Western counties	43.50	-109.57	6

Table 4-2. The isotopic delineation of Burrowing Owl collection areas across study region as determined by Tukey's HSD analyses. Collection areas with the same combinations of sub-set classifications from Tukey's HSD analyses of hydrogen, carbon and nitrogen stable-isotope ratios were grouped (alpha codes). Mean, standard deviation and 95% confidence intervals for natal Burrowing Owl feathers are provided. ‡Values for western Texas / northern Mexico south to north-central Mexico were not determined as feathers were not collected in these areas. However, the high number of wintering owls with values more D_n-enriched than collection areas in the southern US states indicates that breeding populations may be located in the areas labelled R-U in Figure 4-1. Note that the δD_n value of central Mexico (Q) is more D_n-depleted than the estimated value of areas to the north. Currently, little is known about the summer isotope values in this region. The presented δD_n values that go against the gradient presented in this paper may be explained by the topography and precipitation cycles in central Mexico. More investigation is required.

		Tukey's HSD		**δD_n‰**			**$\delta^{13}C$‰**		**$\delta^{15}N$‰**	
Collection Site	**Alpha-code**	**Sub-set (H, C, N)**	***n***	**Mean**	**SD**	***n****	**Mean**	**SD**	**Mean**	**SD**
Hanna Region, AB	A1	1,b,x	18	-115	5.1	12	-23.0	0.8	10.6	2.0
Eastern Irrigation District, AB	A2	1,b,x	20	-114	4.4	14	-22.8	0.8	11.7	0.5

Grasslands National Park, SK	B	2,b,x	12	-106	4.7	11	-22.6	0.6	10.3	1.0
Regina Plain, SK	C	2,b,y	6	-102	6.0	6	-22.5	1.0	13.0	1.4
Alameda/Santa Clara Cos., CA	D	3,b,z	10	-97	3.2	8	-23.6	1.0	15.6	0.6
San Jose Airport, CA	E	3,a,y	10	-95	4.9	10	-24.6	0.4	12.4	0.8
Fort Belknap I.R., MT	F	3,b,x	6	-95	8.5	3	-21.5	0.5	9.2	0.7
South-eastern Counties, WA	G	3,c,x	10	-94	9.7	10	-19.5	1.9	9.4	1.2
Little Missouri NG, ND	H1	4,a,w	6	-89	4.4	6	-22.1	0.7	8.3	1.0
Western Counties, WY	H2	4,a,w	9	-87	8.4	6	-22.4	1.4	8.4	0.7
Lamoore NAS, CA	I1	4,a,x	3	-88	1.0	3	-22.2	0.3	10.0	1.4
Carrizo Plain, CA	I2	4,a,x	5	-85	2.8	5	-21.9	0.5	9.7	0.2
Salton Sea, CA	J	4,b,z	7	-88	5.9	5	-20.2	0.8	14.8	1.1
Buffalo Gap N.G., SD	K	5,b,x	7	-79	2.5	6	-21.5	0.5	9.9	1.1
South-eastern Region, NV	L	5,c,x	3	-72	4.9	3	-19.5	0.2	9.7	0.3

Western Region, KS	M	6,c,w	3	-63	2.3	3	-17.9	1.5	7.8	0.8
Tucson Region, AZ	N	6,c,x	10	-66	6.9	4	-17.2	1.0	10.6	1.2
Las Cruces Region, NM	O	7,c,x	11	-60	5.7	11	-16.8	1.3	10.7	1.2
Lubbock, TX	P	7,c,y	6	-56	5.7	6	-15.4	0.8	12.7	0.8
Central Mexico	Q	7,d,x	7*	-60	7.1	4**	-14.5	1.7	8.5	1.2
Western TX to Central MX	R-U	-	0	-40‡	-	0	-	-	-	-
South-western Region, ID***	-	-	13	-92	14.9	13	-19.4	2.9	11.3	1.6

*Feathers from local Barn Owls and urban pigeons analyzed

**Feathers from local Barn Owls analyzed

***Only feathers from after-hatch-year birds were available. These results were not included in the isotope dataset.

Table 4-3. Long distant migrants as determined by stable-isotope tracking. Three samples from Texas were relatively D_n depleted, but did not fall within the δD_n parameters of the most northern regions of Canada.

Collection Site	Feather Type	Date of Collection	Alpha-code	δD_n‰	$\delta^{13}C$‰	$\delta^{15}N$ ‰	Summer Origin
Mexico							
Northern Veracruz State*	Primary	31/01/01	C	-106	-22.2	13.5	Regina Plain, SK
Leon Zoo, Guanajuato	Tail	18/11/99	A	-116	-21.9	13.6	Hanna Region, AB**
Irapuato, Guanajuato	Tail	19/11/99	C	-106	-22.4	13.3	Regina Plain, SK
Irapuato, Guanajuato	Body	14/11/99	B	-104	-22.1	10.5	Grasslands N.P., SK
Lago Chapala, Jalisco	Body	26/01/00	C	-100	-22.6	13.9	Regina Plain, SK
Irapuato, Guanajuato	Body	08/02/01	F	-96	-22.1	11.1	Ft. Belknap I.R., MT

Texas							
Near McAllen*	Tail	10/02/00	C	-104	-21.9	14.5	Regina Plain, SK
Nueces County	Tail	16/02/00	A	-111	-22.0	11.1	Southern Alberta
Nueces County	Tail	16/02/00	?	-92	-20.9	8.1	Southeast Washington?
Agua Dulce, Nueces Co.	Tail	16/12/00	?	-90	-18.1	11.5	MT/ND/WY?
Perry Fdn., Nueces Co.	Tail	28/01/02	?	-89	-18.9	8.8	ND/WY?

*Feathers collected from radio-tagged or banded birds with known origins.

** The depleted value may be associated with the northern portion of the Burrowing Owl range in Alberta.

Table 4-4. Feather types collected from wintering Burrowing Owls.

Location	Flight Feather	Body Feather
Mexico	43	88
Texas	20	13
New Mexico	4	1

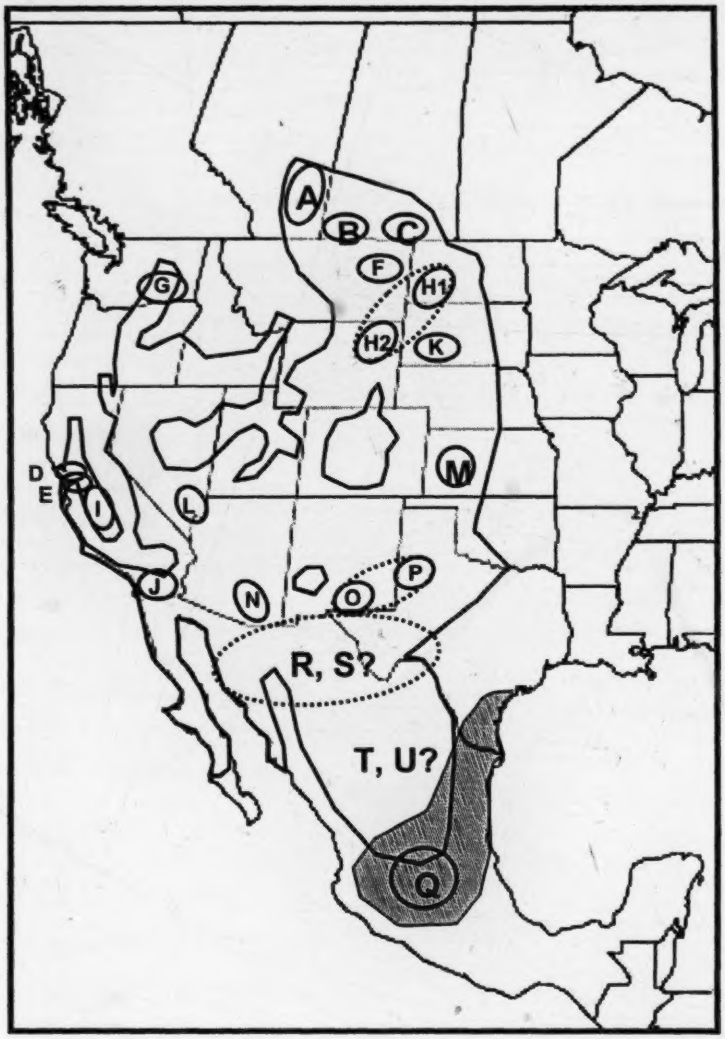


Fig. 4-1. Feather collection regions of natal Burrowing Owls as determined by GLM analyses and post-hoc Tukey's HSD tests. The light shaded area represents the current range of the western Burrowing Owl (adapted from Wellicome and Holroyd 2001). The dark shaded area represents where winter collections were made for this study. Homogenous regions containing multiple collection sites are designated with letters. Sections designated R through U represent areas where the possible enriched δD_n and $\delta^{13}C$ values may be located and where feathers were not obtained.

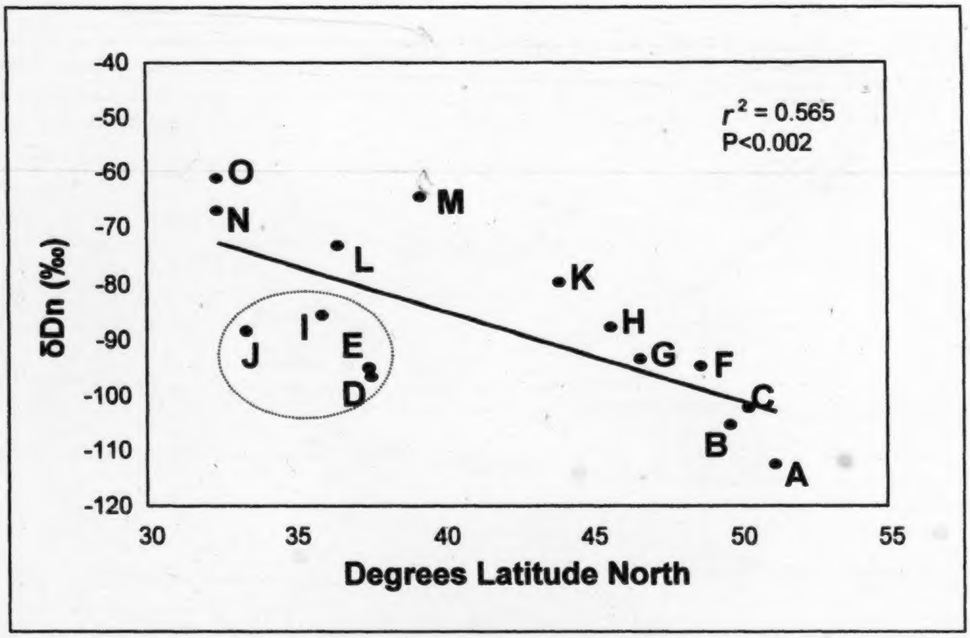


Fig. 4-2. The relationship between δD_n values of Burrowing Owl feathers and the latitude of the collection sites. Refer to Table 4-2 for location names. Sites with the same alpha-code were grouped together. Sites within the hatched circle are located in California.

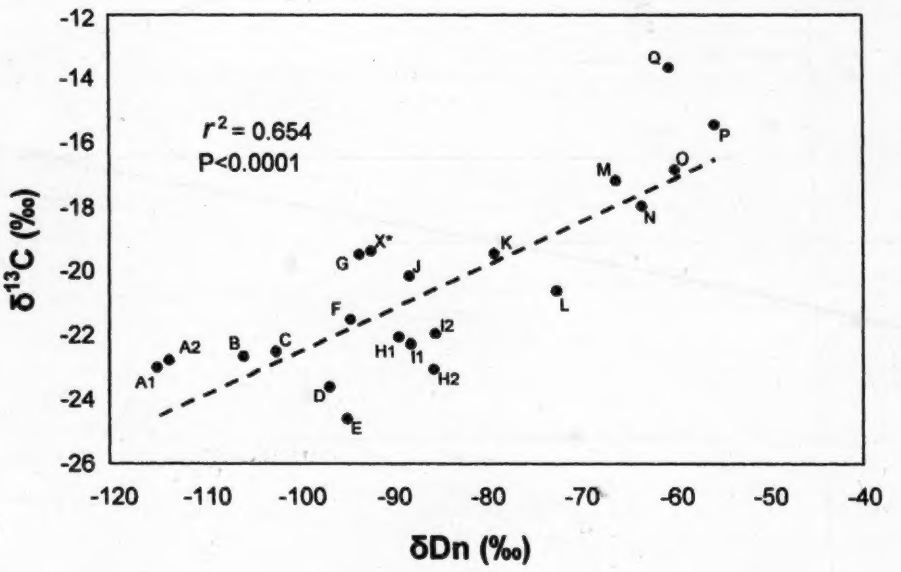


Fig. 4-3. The relationship between δD_n and $\delta^{13}C$ values of Burrowing Owl feathers from summer collection sites. Bars are ± 1 SD. Refer to Table 4-2 for location names. *Value ranges for Idaho are based on feathers from after-hatch year owls.

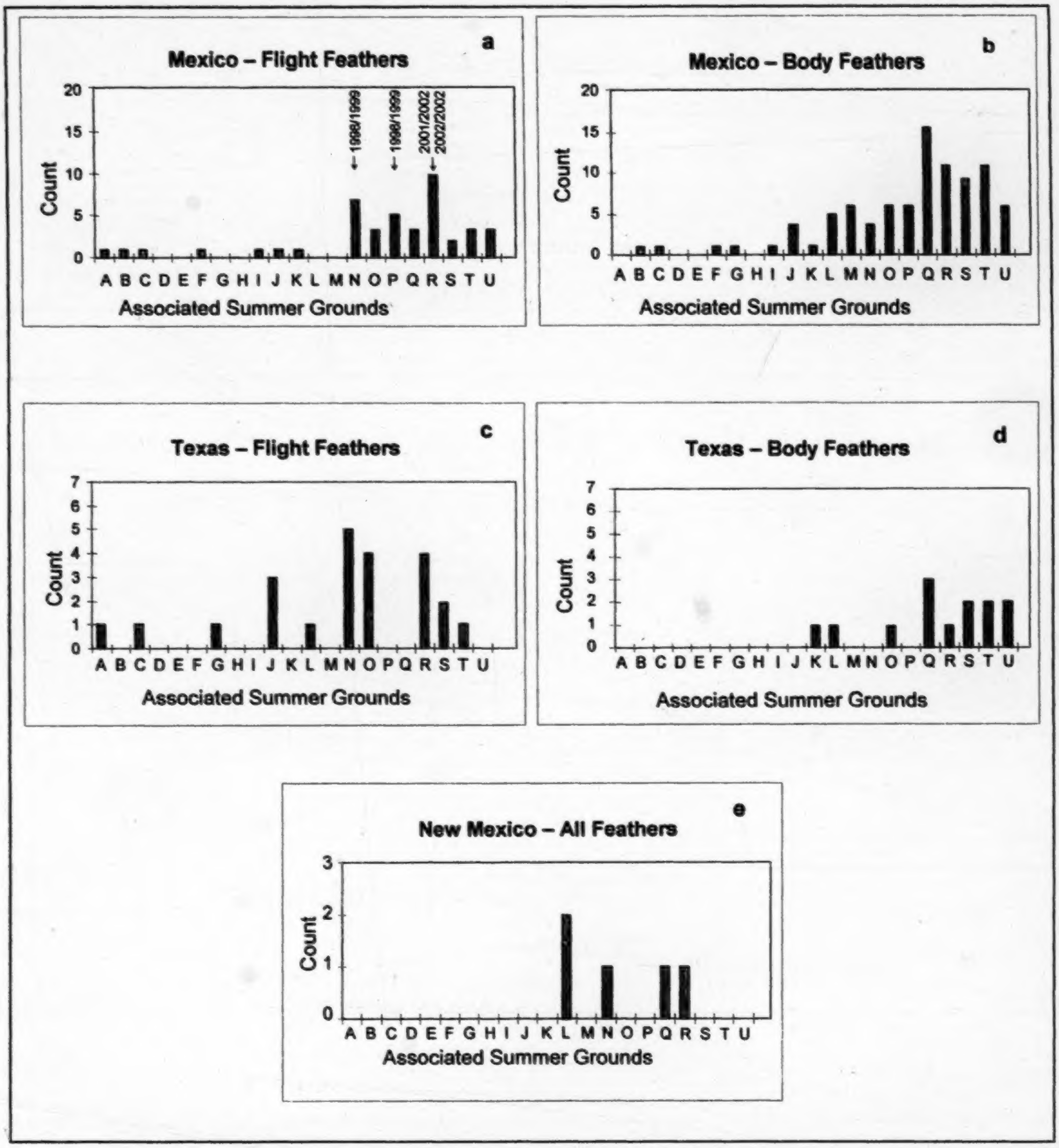


Fig. 4-4. Distribution of migration links between natal/breeding grounds and wintering collection sites in Mexico (a and b), southern Texas (c and d) and New Mexico (e). Letters along the [illegible]axis refer to areas supporting populations from which migrants may have originated the previous summer. Refer to Table 4-2 and Figure 4-4 for locations.

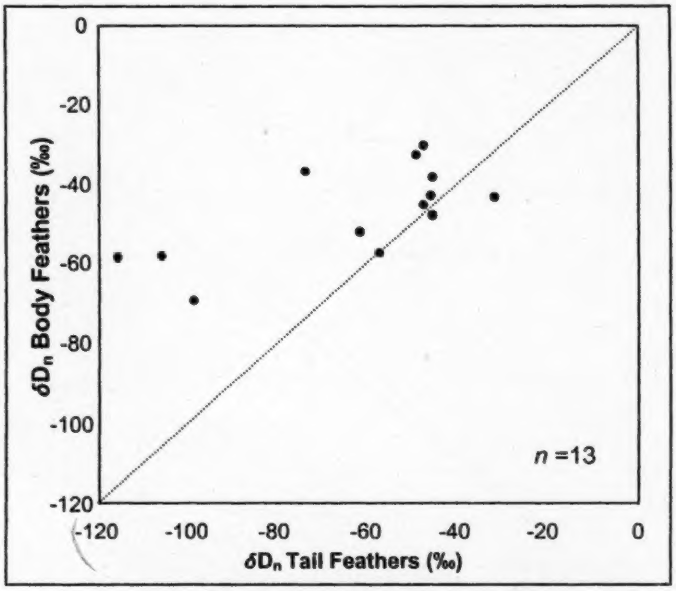


Fig. 4-5. Comparison of δDn values between body and tail feathers collected from individual owls.

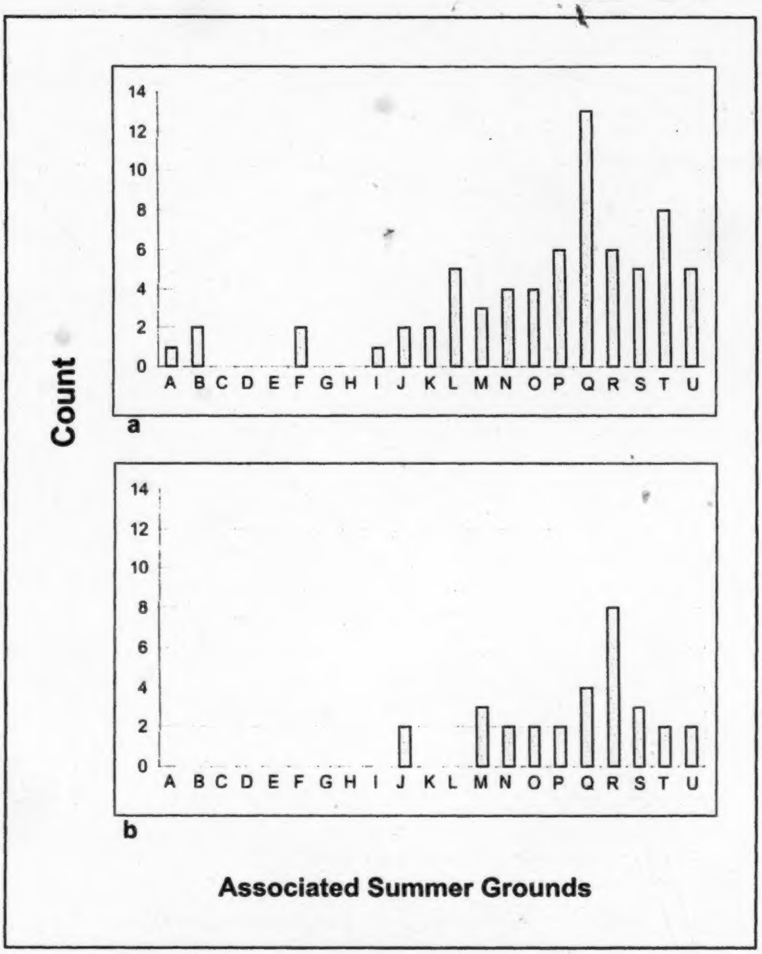


Fig. 4-6. Comparison between summer origins between feathers collected in Guanajuato (a) and Guadalajara (b) States in Mexico. Letters along the x-axis refer to areas supporting populations from which migrants may have originated the previous summer. Refer to Table 4-2 and Figure 4-4 for locations. *Both flight and body feathers were used in this comparison.

LITERATURE CITED

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of Lesser Snow Goose Diets and winter distribution using stable-isotope analysis. Journal of Wildlife Management 57:49-54.

Arrowood, P.C., C.A. Finlay, and B.C. Thompson. 2001. Analysis of Burrowing Owl populations in New Mexico. Journal of Raptor Research 35:362-370.

Brown, N.L. 2001. The howdy owls of Arizona: a review of the status of *Athene cunicularia*. Journal of Raptor Research 35:344-350.

Caccamise, D.F., L.M. Reed, P.M. Castelli, S. Wainwright, and T.C. Nichols. 2000. Distinguishing migratory and resident Canada Geese using stable-isotope analysis. Journal of Wildlife Management 64:1084-1091.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry, and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109:132-141.

Chamberlain, C.P., S. Bensch, X. Feng, S. Åkesson, and T. Andersson. 2000. Stable-isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. Proceedings of the Royal Society of London 267:43-48.

Cherel, Y., K.A. Hobson, and H. Weimerskirch. 2000. Using stable-isotope analysis of feathers to distinguish moulting and breeding origins of seabirds. Oecologia 122:155-162.

Cooke, F., G.J. Robertson, C.M. Smith, R.I. Goude, and W.S. Boyd. 2000. Survival, emigration and winter population structure of Harelquin Ducks. Condor 102:137-144.

Cormie, A. B., H. P. Schwarcz, J. Gray. 1994. Relation between hydrogen isotopic ratios of bone collagen and rain. Geochimica et Cosmochimica Acta 58:377–391.

Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus 16:436-468.

Duxbury, J.M. 1998. An application of stable-isotope ecology to the study of raptor diets. MSc thesis, University of Alberta, Edmonton, Alberta, Canada. 150 pp.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic composition. Limnology and Oceanography 33:1182-1190

Graves, G.R., C.S. Romanek, and A.R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proceedings of the National Academy of Science 99: 8096–8100.

Hebert, C.E. and L.I. Wassenaar. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. Environmental Science & Technology 35: 3482-3487.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue dependent stable-isotope models. Marine Ecology Progress Series 95:7-18.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using 13C and 15N analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K.A. and L.I. Wassenaar . 1997. Linking breeding and wintering grounds of neotropical migration songbirds using stable isotopic analysis of feathers. Oecologia 109:142-148.

Hobson, K.A., L.I. Wassenaar, and O.R. Taylor 1999. Stable-isotopes (δD and δ^{13}C) are geographic indicators of natal origins of monarch butterflies in eastern North America. Oegologia 120:397-404.

Hobson, K.A., R.B. Brua, W.L. Hohman, and L.I. Wassenaar. 2000. Low frequency of "double molt" of remiges in Ruddy Ducks revealed by stable-isotope: Implications for tracking migratory waterfowl. Auk 117:129-135.

Hobson, K.A. and L.I. Wassenaar. 2001. Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. Ecological Applications 11:1545-1553.

Hobson, K.A., K.P. McFarland, L.I. Wassenaar, C.C. Rimmer, and J.E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable-isotope analyses of feathers. Auk 118:16-23.

Holroyd, G.L., R. Rodríguez-Estrella, and S.R. Sheffeild. 2001. Conservation of the Burrowing Owls in western North America: issues, challenges and recommendations. Journal of Raptor Research 35:399-407.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216-221.

Kharaka, Y.K. and W.W. Carothers 1980. Oxygen and hydrogen isotope geochemistry of deep basin brines. Pages 305-360 in Handbook of Environmental Isotope Geochemistry. (P. Fritz and J.C.H. Fontes, Eds.), Amsterdam.

King, R.A. and J.R. Beltoff. 2001. Post-fledging dispersal of Burrowing Owls in southwestern Idaho: characterization of movements and use of satellite burrows. Condor 103:118-126.

Körner, C., F.D. Farquhar, and S.C.Wong. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia 88:30-40

Lajtha, K. and J.D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. Pages 1-21 *in* Stable-isotopes in ecology and environmental science. (K. Lajtha and R.H. Michener, Eds.), Blackwell, Oxford.

Marti, C. 1992. Barn Owl (Tyto alba). *In* No.1 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Meehan, T.D., C.A. Lott, Z.D. Sharp, R.B. Smith, R.N. Rosenfield, A.C. Stewart, and R.K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. Condor 103:11-20.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53-63.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochemica Cosmochemica Acta 48:1135-1140.

Poulin, R.G., K. Scalise, and L.D. Todd. 1999. Saskatchewan Burrowing Owl Recovery Project: A synthesis of research 1994-1998. Saskatchewan Environment and Research Management Report, 22 pp.

Poulin, R.G., T.I. Wellicome, and L.D. Todd. 2001. Synchronous and delayed numerical response of a predatory bird community to a vole outbreak on the Canadian prairies. Journal of Raptor Research 35:288-295.

Rubenstein, D.R., C.P. Chamberlain, R.T. Holmes, M.P. Ayres, J.R. Waldbauer, G.R. Graves, and N.C.Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. Science 295: 1062-1065.

Schimmelmann, A. 1991. Determination of the concentration and stable isotopic composition of nonexchangeable hydrogen in organic matter. Analytical Chemistry 63:2356-2459.

Shearer, G., D.H. Kohl, and S.-H. Chien. 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America Journal 42:899-902.

Shearer, G., Kohl, D.H., and Virginia, R.A. 1983. Estimates of N_2-fixation from variation in the natural abundance of ^{15}N in Sonoran Desert plants. Oecologia, 56: 365-373.

Schmutz, J.K. 1997. Selected mircrohabitat variables near nests of Burrowing Owls compared to unoccupied sites in Alberta. Pages 80-83 *in* The Burrowing Owl, its biology and management including the proceedings of the first international symposium. (J.L. Lincer and K. Steenhof, Eds.), Journal of Raptor Research Report 9.

Schulze, E.D., F.S. Chapin, III, and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406-412.

Sheppard, S.M.F. 1986. Characterization and isotopic variations in natural waters. Pages165-177 *in* Reviews in Mineralogy Vol. 16:Stable-isotopes in High Temperature Geological Processes (J.W. Valley, H.P. Taylor, and J.R. O'Neil, Eds.), Mineralogical Society of America, BookCrafters Inc., Chelsea, MI.

Sissons, R.A., K.I. Scalise, and T.I. Wellicome. 2001. Nocturnal foraging and habitat use by male Burrowing Owls in a heavily cultivated region of southern Saskatchewan. Journal of Raptor Research 35:304-309.

Todd, L.D. 2001. Dispersal patterns and post-fledging mortality of juvenile Burrowing Owls in Saskatchewan. Journal of Raptor Research 35:282-287.

USGS (United States Geological Survey). 2003a. Non-game banding records 1955 – 2002. [online] URL:http://www.pwrc.usgs.gov/bbl/homepage/spec.htm#3780]

USGS (United States Geological Survey). 2003b. Breeding bird survey summary and analysis – winter distribution maps (CBC) [online] URL:http://www.mbr-pwrc.usgs.gov/bbs/cbcra/h3780ra.html

Van der Merwe, N.J., J.A. Lee-Throp, J.F. Thackeray, A. Hall-Martin, F.J. Kruger, H. Coetzee, R.H. Bell, and M. Lindeque. 1990. Source-area determination of elephant ivory by isotopic analysis. Nature 346:744-746.

Vogel, J.C., B. Eglinton, and J.M. Auret. 1990. Isotope fingerprints in elephant bond and ivory. Nature 346:747-749.

Wassenaar, L.I. and K.A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. Proceedings of the National Academy of Science 95: 15436-15439.

Wassenaar L.I. and K.A. Hobson. 2000. Evaluating the use of stable-carbon ($\delta^{13}C$) and H (δD) isotope ratios in feathers to infer breeding origins of Red-winged Blackbirds. Ecological Applications 10:911-916.

Wassenaar, L.I. and K.A. Hobson 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. Environmental Science and Technology 35:1845-1850.

Wellicome, T.I. 2000. The effects of food on reproduction in Burrowing Owls (*Athene cunicularia*) during three stages of the breeding season. Ph.D. dissertation, University of Alberta, Edmonton, AB Canada.

Wellicome, T.I. and E.A. Haug. 1995. Second update of status report on the Burrowing Owl (*Speotyto cunicularia*) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON Canada.

Wellicome, T.I. and G.L. Holroyd. 2001. The second international Burrowing Owl symposium: background and context. Journal of Raptor Research 35:269-273.

Chapter 5

Large-scale dispersal dynamics of Burrowing Owls as determined by stable-isotope analysis[4]

The western Burrowing Owl (*Athene cunicularia hypugaea*) is declining throughout its range across western North America (James and Espie 1997, Sheffield 1997, Holroyd et al. 2001). In Canada, the decline of Burrowing Owls has been identified for over 20 years (Fyfe 1977, Hjertaas et al.1995, Kirk and Hyslop 1998). The number of breeding pairs of Burrowing Owls in Canada is declining by a rate of over 20% per year (Skeel et al. 2001, Wellicome and Holroyd 2001). Saskatchewan's Operation Burrowing Owl program indicates a 95% decline from 1988 to 2000 (Skeel et al. 2001).

The analysis of population parameters and ultimately the development of models may be key requirements to determine the proximate causes of the decline of Burrowing Owl populations (Holroyd et al. 2001). Research has indicated that the number of Burrowing Owls is in decline because productivity, survival, and recruitment rates are low (Blus 1996, James et al. 1997, Schmutz 1997, Wellicome 1997a, Wellicome et al. 1997b, Wellicome 2000, Poulin et al. 2001, Todd 2001, Holroyd et al. 2001). Hoyt (2001) attempted to determine the survival rates for populations in Alberta, Saskatchewan and Manitoba. However, an admitted shortcoming of the modeling process was that a measure of permanent emigration was not available. Therefore, the survival rates that were determined were considered "apparent survival" under the assumption that a proportion of the individuals were not detected due to permanent emigration (Lebreton et al. 1992, Chase et al. 1997, Marshall et al. 2000, DiQuinzio et al. 2001, Johnson et al. 2001, Sillett and Holmes 2002, Fernandez et al. 2003). Accurate Burrowing Owl population modeling will require the separation of inter-year mortality from permanent emigration (Holroyd et al. 2001). Estimates of the rates of survival or mortality would be more accurate with the determination of permanent emigration rates. Unfortunately, information regarding natal or breeding dispersal is limited for Burrowing Owls (Holroyd et al. 2001), as inter-year mark and recapture recoveries are relatively rare in any population with low recruitment rates (Lutz and Plumpton 1999, Walters 2000) or high dispersal rates.

---

[4] *This chapter has been formatted for submission to Condor.*

Since physical evidence of bird mortality is rarely found, rates of permanent emigration and mortality are difficult to separate (Haas and Sloane 1989, Wellicome 1997b, Koenig et al. 2000). In addition, the sizes of study areas are limited due to political, temporal, logistical and monetary reasons. Historically, Burrowing Owls that disperse out of study sites are hard to follow (Leupin and Low 2001, Martell et al. 2001). The result is that the frequency and distance of dispersals must be estimated when individuals fail to return (Wellicome 1997b, Leupin and Low 2001). However, how can the estimation of "apparent dispersal" be conducted without knowledge of the true rates of mortality and emigration?

Amongst other causes, declines in Burrowing Owl populations have been attributed to habitat loss and fragmentation from both agriculture and urban encroachment (Uhmann et al. 2001, Jones and Bock 2002). Habitat fragmentation usually conjures images of clear-cut forests; however, grasslands are one of the most threatened and degraded habitats in North America (Samson and Knopf 1994, Vickery and Herkert 2001, Jones and Bock 2002). Conversion to croplands, overgrazing by livestock, the spread of exotic species, and disrupted fire regimes are historical changes that have negatively impacted most grassland bird populations (Knopf 1994, Saab et al. 1995, Vickery and Herkert 1999).

Burrowing Owls require fossorial mammals to create nesting burrows. Across the Great Plains, nesting burrows for the owls are provided by ground squirrels (*Spermophilus* spp.) or Black-tailed Prairie Dogs (*Cynomys ludovicianus*) burrows, Badger (*Taxidea taxus*) excavations and occasional fox (*Vulpes* spp.) dens (Desmond and Savidge 1996, Plumpton and Lutz 1993, Arrowood et al. 2001, Wellicome 1997b, Murphy et al. 2001, Orth and Kennedy 2001, Restani et al. 2001, Sheffield and Howery 2001, Sidle et al. 2001, VerCauteren et al. 2001, but see Korfanta et al. 2001, Klute et al. 2003). Burrowing Owls benefit from an association between ground squirrels / prairie dogs with the provision of shelter, predator surveillance, alarm calls, an alternate prey source for predators, and a reduction in vegetation height for better visual detection of predators (Desmond et al. 2000). Higher numbers of burrows provide non-nest satellite burrows that are especially important during the post-fledging period for shelter from predators and inclement weather, prey caching, and the initiation of dispersal (Desmond et al. 2000, King and Belthoff 2001, Todd 2001, Klute et al. 2003). Since about 1900, suitable habitat across the entire range of Black-tailed Prairie Dog colonies has been reduced by approximately 94-99% (Barko 1997, Wuerthner 1997). The loss of Black-tailed Prairie Dog colonies due to the conversion to cropland, urban encroachment, eradication (both systematic and recreational) and sylvanic plague (*Yersinia pestis)* has meant a decline in Burrowing Owl nesting habitat in the Great Plains (Orth and Kennedy 2001, Restani et al. 2001, Roach et al. 2001, Sheffield and Howery 2001, Sidle et al. 2001, VerCauteren et al. 2001, Jones and Bock 2002). If suitable Burrowing Owl nesting habitat is associated with the fragmented patches of prairie dog habitat (Miller 1994, USFWS 2001), the attributes and composition of the fragments potentially play an important role in owl dispersal and population persistence (Wiens 1996).

Within populations, Burrowing Owl nesting sites near the core of populations persist due to the greater probability of burrow re-occupation from recruits from surrounding nest sites. Nest sites located at the periphery of a population have a lower probability of re-occupation (Warnock and James 1997). At a greater scale, peripherally located populations may face greater persistence difficulties relative to centrally located populations. Peripheral populations are in danger of becoming extirpated and core populations are threatened to become peripheral populations (De Smet 1997). Generally, at large geographical scales, animal populations at the edge of their range are more sensitive to habitat alternation, quality, and configuration of habitat fragments than central populations (Hanski and Gilpin 1997, Mönkkönen and Reunanen 1999, Araújo and Williams 2001, Kyle and Strobeck 2002, Roslin 2002). Populations have recently become extirpated in Manitoba (DeSmet 1997) and Minnesota (Martell *et al.* 2001). Breeding Burrowing Owls have not been seen in British Columbia since the 1960s, with the last owl sighting occurring in 1979 (Leupin and Low 2001). Shyry et al. (2001) documented a decline of over 90% in nest density in Alberta's most northern population between 1991 and 1997. The authors suggest this Alberta population is facing probable extirpation. In addition, release programs along the northern and eastern edges of their range in Canada have had no success in Manitoba (De Smet 1997), British Columbia (Leupin and Low 2001), and Saskatchewan (D.L. Todd unpublished data). Releases of Burrowing Owls in Minnesota between 1986-1990 resulted in no returns or recoveries (Martell et al. 2001). Burrowing Owl populations at the northern and eastern periphery of their range appear to be unsustainable.

Metapopulation theory arose in an attempt to explain the relationships between groups of populations living in disassociated habitats (Levins 1970, Hanski and Gilpin 1997, Hanski 1999). The characteristics of population dynamics associated with metapopulations can be used to discuss the potential of sustaining a population between habitat fragments situated across a landscape (Kareiva 1987, Hess 1996, Kareiva and Wennergren 1995, With 1997). The functional connectivity of remnant habitat depends on the ability of animals to cross potentially inhospitable matrices between patches to supply diminishing populations or re-colonize patches where populations are no longer persisting (Fahrig 1997, 1998, 1999, With 1999). Current metapopulation theory has moved away from viewing matrices as being completely inhospitable (Vandermeer and Carvajal 2001, Gobeil and Villard 2002). Unsuitable habitat matrices, such as crops and fallow (Sissons et al. 2001), may not impose dispersal barriers because of a Burrowing Owl's ability to migrate. However, at large regional scales, suitable habitat may occur as patches of grasslands divided by agriculture or urban encroachment. Therefore, matrices in fragmented grasslands may play an important role in the dispersal patterns of Burrowing Owls at large scales.

Traditionally defined metapopulations are sustained with the re-colonization of extirpated sub-populations. In order for these processes to occur, the population trends of the sub-populations must be asynchronous (Wiens 1996). Most Burrowing Owl "sub-populations" are currently in synchronous decline (Holroyd et al.2001). Extinct Burrowing Owl "sub-populations" in Manitoba and Minnesota are not being re-colonized. Therefore, traditional metapopulation theory may not be applicable to the owls (Plissner and Haig 2002). Whether or not metapopulation theory applies to Burrowing Owls, the examination of the processes that are associated with metapopulation dynamics, such as dispersal and re-colonization between "sub-populations" is important to understanding the species' population dynamics and how those dynamics are linked to landscape configuration (Martin et al. 2000).

The effects on dispersal due to landscape alteration, fragmentation and configuration are hard to predict without the initial determination of dispersal patterns (Walters 2000). Unfortunately, knowledge of large-scale dispersal of many organisms is difficult to obtain (Wiens 1994, 1996, Kareiva and Wennergren 1995, Harrison and Bruna 1999, Burke and Nol 2000, Sutherland et al. 2000, Walters 2000, King and Belthoff 2001). Most of the larger scale empirical studies conducted to test spatial, landscape models have been limited to presence / absence data (McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999). Even though such studies can be conducted over a span of years, they are in essence yearly snap-shots of the population that must be pieced together in an attempt to determine how the population is changing across the landscape. For a more dynamic picture of how a population is reacting to the configuration of landscapes, the movements of animals between at least two points should be monitored.

It is possible to track migrant birds between locations using telemetry or mark and recapture techniques. VHF Radio-tracking limits sample sizes due to logistics, time and expense. Transmitter batteries have a finite life, which also limits the temporal scales of studies. In addition, VHF radio-tracking may be able to ascertain when a bird disperses, but the determination of where the bird goes may be limited to the size of a study area and the transmission distance of transmitter. The mass and the operational expense of satellite transmitters severely limit their effectiveness. Mark-recapture methods such as bird banding are relatively less expensive, but the rarity of the recapture of migratory birds severely limits the sample size. If band recoveries are uncommon, important long-distance dispersal events are rarely detected (Koenig et al. 1996). Results of mark-recapture studies that may be biased against inter-population dispersal can only be evaluated by data acquired by means other than direct observation (e.g. genetic signatures; Koenig et al. 2000, Arguedas and Parker 2000). To date, genetic analyses have been unsuccessful in both the delineation of Burrowing Owl populations and the determination of rates of inter-population mixing in western North America (Desmond et al. 2001, Korfanta et al. 2001). In this study, stable-isotope analysis (SIA) is evaluated as another biochemical method of potentially delineating Burrowing Owl populations and tracking inter-year dispersal patterns.

SIA was originally used by geochemists in fields such as hydrology, palaeoclimatology, and for the examination geomorphological pathways (Schiegal 1972, Kharaka and Carothers 1980, Muehlenbachs 1986, Sheppard 1986, Ehleringer and Rundel 1989, Sternberg 1989). Geochemists were first to realize that stable-isotope ratios changed in biological systems and began to determine how and why the ratios changed (Wickman 1952, Craig 1953, Park and Epstein 1960). The development of SIA helped determine the relative amount of isotopes in organic and inorganic matter, how these ratios are altered and finally, how they could be used in the investigation of natural systems. Because stable-isotopes do not decay, they can be used to investigate biological processes since they can be traced through natural systems using mass spectrometry (Peterson and Fry 1987, Ehleringer and Rundel 1989, Lajtha and Marshall 1994).

The study of migratory animals with SIA provides a relatively new method that can trace migrants back to their natal or breeding grounds without having been previously banded (Hobson 1999). Hydrogen isotope ratios (δD) in precipitation are altered (fractionated) by temperature change, distance from maritime systems and altitude (Dansgaard 1964, Kharaka and Carothers 1980, Sheppard 1986). These ratios exist in predictable patterns across North America and Chamberlain et al. (1997) and Hobson and Wassenaar (1997) were first to demonstrate that the hydrogen isotope ratios are not significantly altered though food chains and are found in correlated continental patterns in the feathers of birds. The average carbon isotope ratios (δ^{13}C) of ecosystems can differ based on the dominant type of photosynthesis (C3, C4, and CAM) of plants or differences in enzymatic reactions and water use efficiency at varying levels of relative humidity (Craig 1954, Park and Epstein 1960, Smith and Epstein 1971, DeNiro and Epstein 1978, Körner et al. 1991). Arid climates can cause denitrification and enriched levels of ^{15}N in soils relative to more humid regions

(Van der Merwe et al. 1990, Vogel et al. 1990, Chamberlain et al. 2000). Nitrogen isotope ratios in plants depend on the type of nitrogen fixing process used by the plants and upon soils that have variable nitrogen dynamics (Shearer et al. 1978, Schulze et al. 1994, Michelsen et al. 1996, Graves et al. 2002). Anthropogenic enrichment associated with agriculture can also create differences in nitrogen isotope ratios in plants and animals (Duxbury 1998, Hebert and Wassenaar 2001). All of the above-mentioned causes of fractionation produce large-scale, continental patterns that can be ultimately detected in animal tissues through SIA (Hobson 2002).

SIA was used to investigate inter-year movements of Burrowing Owls between regions in the Northern Great Plains. The objectives of this study were to 1) determine if Burrowing Owls have regular long distance dispersal movements (natal or breeding); 2) determine proportion of owls that dispersed and the direction and distance of the dispersal between breeding seasons; and 3) evaluate the net difference in dispersal between Canada and the US. Measurements of dispersal will aid in the estimation of immigration and emigration rates for population modelling. The determination of large-scale dispersal patterns and their relative proportions is an important step towards the establishment of the exchange rates between regions containing breeding Burrowing Owls.

METHODS

SAMPLE COLLECTION

Nestling Feather Dataset. In Chapter 4, wintering Burrowing Owls were traced back to their summer origins with the use of a stable-isotope, reference dataset. Burrowing Owl nestling feathers were analyzed to create the dataset. Nestling feather samples were collected from across the Burrowing Owl breeding range of western North America. The same dataset from Chapter 4 was used in this current chapter which focuses on return rates and dispersal of Burrowing Owls between regions in the Northern Great Plains.

Requests for feather samples were sent to researchers conducting field studies across the range of the Burrowing Owls. For the creation of the reference dataset, feathers were collected from nestlings by field researchers that visited nests. Burrowing Owl nests can be approached on foot and do not require a climb to gain access. By the time young Burrowing Owls are seen above ground they have started to grow in their juvenile plumage. These factors meant that the plumage stage from which feathers were collected from nestlings was relatively consistent. For the creation of an isotope reference dataset, the sample collection consisted mainly of juvenile body feathers complemented with juvenile down or flight feathers. The collection commenced 1997 and continued until 2003 across the majority of the species' western North American breeding range. Mean isotope values of nests were used in statistical analyses in instances where more than one owl from a single nest was analyzed. For this study, the SIA results from a subset of feathers analyzed in Chapter 4 were used for the reference dataset (Collection sites A, B, C, F, H, and K; Table 4-1, Figure 4-1).

After-hatch-Year Burrowing Owl feathers. The collection of feathers from nesting Burrowing Owls that were at least a year old began in 1998 and continued until the fall of 2002. Burrowing Owls are known to go through a complete moult of all remiges and retricies on the breeding grounds (Haug et el. 1993). Therefore, isotopes of flight feathers were considered indicative of where a breeding owl bred or was raised the preceding summer. When possible, owls were trapped and a sample of a tail feather was collected along with a body feather. A primary or tail feather was collected from the remains of two dead owls (2%). The sample collection included 9 (9%) moulted body feathers found near nests and roosts. The body feathers were utilized to increase the sample size. However, the moult cycle of body feathers has yet to be described and some body feathers are moulted on the wintering grounds or possibly on migration (G. Holroyd pers. comm.). Therefore, the SIA results for body feathers were used in analyses with caution.

Test of Confidence. A blind analysis test was conducted to establish confidence in the isotope tracking process. Feathers were obtained from two wintering Burrowing Owls located by radio-telemetry and a band recovery. These feathers were analysed to see if their isotope values matched the parameters of the areas from which they originated. The samples were analyzed blindly to control analytical bias.

FEATHER ANALYSES

Feathers were first washed with a mild solution of detergent and water. Surface oils and contaminants were removed with a 2:1 solution of chloroform and methanol. Feathers washed with the solution were allowed to dry in a fume hood then weighed. Between 7-10 mg of feather tissue were required for hydrogen analyses, and another 1 mg was required for the carbon and nitrogen analyses. It was assumed that the isotope values in feathers collected from a single nestling were uniform.

Hydrogen. Feathers are almost completely composed of keratin protein. Most of the hydrogen in keratin is inertly bonded to carbon atoms. However, hydrogen atoms are also weakly bonded to the nitrogen and oxygen atoms of the protein molecules. The weak bonds can lead to exchange with hydrogen in ambient water vapour (Schimmelmann 1991). This exchange can introduce erroneous results associated with the transport and storage of samples away from the site where the feathers were grown (Wassenaar and Hobson 2000).

To control the effects of this exchangeability of hydrogen, samples were equilibrated under controlled conditions using a modified method similar to those developed by Schimmelmann (1991) and Wassenaar and Hobson (2000). With the use of a steam chamber, the samples were exposed to water vapour with a known hydrogen isotopic value at 130°± 0.1C for a period of two hours. The samples were then allowed to slowly return to room temperature. Samples were sealed under vacuum and combusted at 850°C for two hours, and were gradually allowed to return to room temperature. The resulting water vapour was reduced to H_2 gas over hot zinc. Hydrogen from the feather samples was analyzed with the use of a duel-inlet, Finnigan-MAT 252 mass spectrometer. Hydrogen isotopic values are reported as δD values and are in parts per thousand (‰) relative to the Vienna Standard Mean Ocean Water (VSMOW) standard. Results were normalized using a scale of standards (VSMOW/GISP/SLAP). Water samples analyzed with each batch of feathers produced a 95% confidence interval of ± 1‰ (n=54). An isotopic fractionation factor of +80‰ was used in calculating the δD values of the non-exchangeable hydrogen (D_n)(equation 2; Hobson et al. 2001). Samples were equilibrated and analyzed randomly in order to minimize the introduction of temporal and isolation biases (Hurlbert 1994).

Carbon and Nitrogen. One mg of a feather sample was placed in tin cups and was combusted in a Robo-Prep elemental analyzer at 1800°C. The resultant CO_2 and N_2 were analyzed with the use of an inter-faced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS). Carbon isotope ratios (δ^{13}C) are expressed relative to the PeeDee Belemite (PDB) international standard. Nitrogen isotope ratios (δ^{15}N) are expressed relative to atmospheric

N_2. Analytical error was measured at ± 0.1‰ and ± 0.3‰ for stable-carbon and nitrogen isotope measurements respectively.

STATISTICAL ANALYSES

A multivariate General Linear Model procedure (GLM) was used to determine if significant variability existed among the isotopic values of the natal feathers across the geographic range of the study. The samples were categorized by collection areas. Each element (H, C, N) was analyzed separately and grouped into homogenous sub-sets of isotopic values by a post-hoc Tukey's HSD (α=0.05). Unique combinations of sub-sets from the three Tukey's HSD analyses were used to differentiate the collection areas. Regression analyses were used to determine if a linear relationship existed between hydrogen and carbon isotope values in the natal feathers, between δD_n values and latitude, and between $\delta^{15}N$ values and latitude. Once the isotope dataset was created, the previous summer location of after-hatch-year Burrowing Owls were estimated by a comparison of the isotope values of the feathers from the the after-hatch-year owls to the parameters of the isotopically delineated collection areas. Statistical analyses were conducted using SPSS v.11.

Once the isotope reference dataset was created, the SIA results of the Burrowing Owls returning from their winter grounds were associated with the isotopic parameters of the collection sites. Those owls with stable-isotope values falling within a standard deviation of the mean isotope values of the area where their feathers were collected were considered returns. Those owls with values falling outside one standard deviation of where their feathers were collected were considered to have dispersed. In cases where the isotope values of returning owls did not fall within the parameters of collection sites, their origins were estimated with the use of the relationship between collection site hydrogen / carbon and hydrogen / latitude as determined in Chapter 4.

TRANS-BORDER DISPERSAL AND EXCHANGE

In order to estimate the relative amount of trans-border exchange of Burrowing Owls between Canada and the US, a simple model had to be created that could be used with a combination of predetermined mortality rates and proportional dispersal rates to be determined by SIA.

The number of Burrowing Owls that return to breed in Canada in a subsequent year (N_{Y+1}) can be represented in the following relationship:

$$N_{Y+1} = N_R - \Delta E \tag{1}$$

Where N_R represents the number of owls that survive the winter and return to breed in Canada:

$$N_R = N_Y - M_{PM} - M_W \tag{2}$$

Where N_Y represents the total post-breeding population in Canada for a given year:

$$N_Y = (A_Y + A/2^*J_Y)$$

Where A_Y is equal to the number of adults in the population in a given year and J_Y is equal to the mean number of fledged juveniles per breeding pair of adults in a given year.

and M_{PM} represents pre-migratory mortality:

$$M_{PM} = N_Y - 0.42(N_Y)$$

and M_W represents the mortality during the winter of the owls that survive to migrate:

$$M_W = M_{PM} - 0.20(M_{PM})$$

Where ΔE is the relative difference in the permanent emigration between Canada and the Montana, North Dakota, and Wyoming region:

$$\Delta E = X_{Can}(N_R) - X_{US}(pN_R) \qquad (3)$$

Where X_{Can} is the proportion of Burrowing Owls in Canada in a given year with origins in the US, and X_{US} is the proportion of Burrowing Owls in the US in a given year with origins in Canada. The variable p is size of the Burrowing Owl population in the US portion of the northern Great Plains in proportion to Alberta and Saskatchewan (currently estimated at 3.5 times).

It should be noted that the relationship represented by equations 1-3 does not depend on a survival rate as determined by band recoveries. Pre-migratory survival rates were determined by casualty rates during summer, radio-telemetry studies (Clayton and Schmutz 1997, Todd 2001). Winter mortality rates were determined by winter telemetry studies in Texas and Mexico (G. Holroyd unpubl. data). Dispersal rates and mortality rates are separated and the effects of each on population change can be studied individually. To estimate the relative amount of trans-border exchange, SIA was used to determine the variables X_{Can} and X_{US}.

RESULTS

ISOTOPE REFERENCE DATA-SET

In Chapter 4, feathers from 161 individual natal Burrowing Owls were analyzed to create the isotope reference dataset used in this study. Of these feathers, 151 (93.5%) were from the juvenile plumage (body feathers, or small samples from flight feathers). Due to limited sample sizes in some collection areas, 10 (6.5%) juvenile down feathers were included.

The mean isotope values of collection sites varied significantly across the range of the Burrowing Owl (GLM *Pillai's Trace* $F_{57,309} = 27.0$, $P<0.0001$). Across the entire range, the collection site mean δD_n values ranged from -115‰ to -56‰ (GLM $F_{19,133} = 45.53$, $P<0.0001$;Table 4-2). The regional mean δD_n values across the northern portion of the Great Plains ranged from -155‰ in Alberta to -79‰ in South Dakota. In general, relatively southern collection sites had comparatively enriched δD_n values, while the northern collection sites had more depleted δD_n values. As Kelly et al. (2002) documented for Wilson's Warbler (*Wilsonia pusilla*), δD values of western Burrowing Owls and latitude were correlated across the their range ($F_{1,13} = 14.19$, $P < 0.002$, $r^2 = 0.522$; Figure 4-2). The D-depletion in feathers (δD_n) relative to δD values of precipitation (Cormie et al. 1994, Wassenaar and Hobson 2001) ranged from approximately 20-30‰ depending on the location of Burrowing Owl sample collection sites.

The variation in mean δ^{13}C values was also considerable across the study area (-24.6 to -17.2‰)(GLM $F_{19,103} = 45.22$, P<0.0001). Although the range of carbon isotope values was smaller than that of the hydrogen isotope values, the carbon isotope values also fell into a gradient with relatively more depleted values associated with the more northern regions (Table 4-2). The collection site mean δ^{13}C values across the northern portion of the Great Plains ranged from -22.8‰ in Alberta to -21.5‰ in South Dakota. The relationship between the δD_n and δ^{13}C values across the continental range of the study was significant ($F_{1,19} = 42.64$, $P < 0.0001$, $r^2 = 0.654$; Figure 4-3).

The Tukey's HSD test grouped the δD_n, δ^{13}C and δ^{15}N values into seven, four and four homogenous sub-sets respectively (Table 4-2). A decrease in the number of sub-sets indicated a decrease in variability in the elemental isotope species across the study range. The sets of Tukey's classifications for each of the three elements were then combined for each region. Those regions with the same three classifications were categorized into groups designated with a single letter. The collection sites in within Alberta (Region A) and between Wyoming and North Dakota could not be significantly separated (Region H, Figure 4-1). The two collection areas in Saskatchewan were not significantly different in δD_n and δ^{13}C values, but were separable by δ^{15}N values.

INTER-REGIONAL MOVEMENTS

One hundred and five samples from after-hatch-year Burrowing owls were available for analysis. The majority of the samples were obtained from collection sites in Alberta and Saskatchewan. After-hatch-year samples were also obtained from Montana, Wyoming and North Dakota. Only samples from hatch-year owls were obtained from South Dakota.

Alberta. The SIA results suggested that 23 of 53 (43%) Burrowing Owls sampled in Alberta had returned to the vicinity of the site they occupied the previous summer. Another 8 (15%) were estimated to have originated in Saskatchewan and 7 (13%) from Montana. The estimated origins of the remaining 13 (25%) were scattered amongst sites south and east of Montana except for two (4%) samples that matched values of the collection site in Washington State. The relatively enriched values of samples indicate a few owls had dispersed great distances between breeding seasons. One sample had an isotope signature consistent with southern Nevada, another (possibly two) with Kansas and a third with eastern Texas or northern Mexico (Figures 5-1a and 5-2a). Two feathers had values as enriched as the Barn Owl and feral pigeon samples collected in central Mexico (see Chapter 4).

Saskatchewan. Of the 26 samples collected in Grasslands National Park, six (23%) had estimated origins within the park and another six were consistent with the isotope parameters of the Regina Plain. The combined 46% that appear to have originated in Saskatchewan the previous year, is consistent with the "return" rate of Alberta (43%) noted above. One (4%) sample had isotope values matching those of Montana, and another six samples had isotope values falling within the parameters of the collection sites in Wyoming / North Dakota (Figures 5-1b and 5-2b). Only two (8%) samples could be traced to Alberta and two samples may have originated in Washington State. Two of the three remaining samples had probable origins in southern New Mexico. The origin of the final sample was estimated to be from Kansas (Figures 5-1b and 5-2b).

Only four samples were available from the Regina Plain. Two of the samples were estimated to have originated in the Regina Plain. One sample seemed to have been grown in Alberta and the other appears to have originated in Montana (Figures 5-1b and 5-2c).

Montana. Three (33%) of the 15 samples collected in the Ft. Belknap I.R. Prairie Dog colony probably originated from within the same colony. Six (40%) had probable origins within Canada; one (7%) from Alberta, two (13%) from Grasslands N.P. and three (20%) from the Regina Plain. The remaining four samples (27%) originated from southern regions such as Kansas, Arizona, Nevada, and eastern Texas / northern Mexico (Figures 5-1c and 5-2d).

Wyoming / North Dakota. Only seven after-hatch-year samples were available for the Wyoming / North Dakota region. Of the seven, two were likely local in origin, two originated in Montana, and one had a depleted δD_n value that fit the parameters of Alberta collection sites (Figures 5-1d and 5-2e). The final two samples had highly enriched δD_n values that suggest these tail feathers were grown as far south as Mexico.

The SIA results indicate that 50 of all 105 after-hatch-year Burrowing Owls remained philopatric to the summer ground of the previous year (Figure 5-3). This would represent a 33% return rate in mark-recapture studies. Based on the broad distance categories in figure 5-3, the mean dispersal distance was 619 km. When four samples that indicated extreme dispersal distances are not included in the calculation, the mean dispersal distance was 520 km, the approximate distance between the Alberta collection area and the Regina Plain or the Ft. Belknap I.R. colony in Montana. Similar to recovery rates based on band returns, the average dispersal distance for females (460 km) was greater than for males (360 km)(Figure 5-4), although this difference was not significant (*t*-test, $t = 2.02$, $p = 0.433$).

TRANS-BORDER DISPERSAL AND EXCHANGE

The third goal of the study was to evaluate the net difference in dispersal between Canada and the US. The SIA results indicated that 42.5% of the Burrowing Owl population of Canada was comprised of owls that originated in a US population the previous summer (Figures 5-2 a-e). Only 25.5% of the Burrowing Owls in the northern Great Plains of the US are comprised of owls originating in Canada the previous summer (Figures 5-2 f-i). However, population estimates indicate that there are approximately 3.5 times as many

Burrowing Owls in the adjacent northern Great Plain states (Montana, North Dakota, Wyoming) than there are in Alberta and Saskatchewan (Wellicome 1997b, Skeel et al. 2001, Klute et al. 2003).

With an estimate of the net exchange of Burrowing Owls that disperse across the Canadian / US border, Equations 1-3 can be used to estimate the net change in Burrowing Owl numbers in Canada in a subsequent year. According to the SIA results Equation 3 becomes:

$$\Delta E = 0.43(N_R) - .026(3.5^*N_R)$$

The post-breeding population of Burrowing Owls in Canada is reduced by approximately 50% by juvenile mortality (Clayton and Schmutz 1997, Todd 2001). Adults are also reduced by post-breeding, pre-migratory mortality. The mortality rate for adult Burrowing Owls in the Hanna region of Alberta was found to be close to 40% in 1995 and 1996 (Clayton and Schmutz 1997). Kaplan-Meier survival estimates for southern Alberta (1998-2000) indicate the mean adult survival rate to be 90% (R. Sissons unpubl. data). If a pre-migratory, adult mortality rate of 25% is used in conjunction with a 50% pre-migratory mortality rate for juveniles; the pre-migratory population would then be reduced by approximately 42%. The number of owls that survive to migrate is further reduced by another 20% as current estimates for winter survival are approximately 80% (G. Holroyd unpubl. data). Since absolute population size varies between regions, the relative amount of dispersal had to be applied against population size. The most recent estimates for population sizes in Alberta (Wellicome 1997b), Saskatchewan (Skeel et al. 2001) and the states of the northern Great Plains (Klute et al. 2003) were adjusted by Breeding Bird Survey trend estimates (Sauer et al. 2003). Data on the relative amount of available habitat does not exist for the northern portion of the Great Plains. It was assumed that proportions of suitable and unsuitable habitat were comparable across the study area. An extrapolation of the above population estimates across the study area produced an approximation that the population of Burrowing Owls in the US portion of the northern Great Plains is currently 3.5 times that of the population in Alberta and Saskatchewan.

If an estimated 500 pairs of Burrowing Owls in Canada produced an average 4.5 chicks per nest (Poulin 2003), the post-breeding population in Canada would be 3250 owls. A 42% reduction due to pre-migratory mortality would reduce the post-breeding population from 3250 to 1875 Burrowing Owls. Winter / migration mortality would decrease the number of potentially returning owls to 1500. The relative difference in the permanent emigration (ΔE) predicts a net loss of another 720 Burrowing Owls from Canada to US populations; 22.2% of the post-breeding population. Therefore, of the 3250 owls of the post-breeding population, approximately 780 are predicted to return to Canada. A return of 780 Burrowing Owls would be a 22.0% decrease from the previous year. Interestingly, current estimates of decline are approximately 22% (Wellicome and

Haug 1995, Skeel et al. 2001, Wellicome and Holroyd 2001). If each breeding pair annually produced 8 young, the number of Burrowing Owls in Canada would increase by 20% per year. If the rate of emigration was equal to the rate of immigration, only 2.4 young per breeding pair would be required to maintain the number of owls in Canada the previous year (Figure 5-7).

DISCUSSION

LONG-DISTANCE DISPERSAL.

The first objective of this study was to determine if Burrowing Owls have regular long distance dispersal movements. The SIA results indicate that while a third of the Burrowing Owls are philopatric, it might be common for others to relocate between summers to breeding grounds separated by hundreds of kilometres. In fact, the magnitude of the mean dispersal distances as determined by SIA is approximately 7-10 times greater than those determined by mark-recapture studies conducted within the confines of a study area (R. Poulin unpubl. data). A few SIA results suggest that some owls may disperse to areas that are separated by over 1000 km. Similar to the findings of mark-recapture studies, females appear to disperse greater distances than males, though again the magnitude of the mean dispersal distances as determined by SIA are far greater than those determined by band recovery studies.

The majority of the long distance dispersals (>500 km) to regions in Canada, as determined by SIA, were from locations on the east side of the continental divide (Figure 5-5), and most appear to fall on a possible migration route to between the Great Plains and an area between southern Texas down to central Mexico. Burrowing Owls banded in Idaho, Utah and British Columbia have been recovered in California and the Baja Peninsula (King and Belthoff 2001). Most recoveries of banded Burrowing Owls that were originally captured on the eastern side of the continental divide have also occurred east of the divide. These recoveries suggest that Burrowing Owls were not typically crossing the continental divide on migration. However, an owl that attempted but failed to breed in southern Arizona in April was subsequently re-trapped at a successful nest in southern Saskatchewan in July of 2003 (Holroyd and Conway unpublished data). The SIA results of feathers from this one-year-old owl indicate it was raised in the region of the July recapture. Therefore, the owl must have crossed the continental divide on both its fall migration and its subsequent spring migration. Also, Burrowing Owls from Canada have been traced to areas west of the continental divide in Mexico by banding, radio telemetry and isotope tracking (Chapter 4, G. Holroyd unpubl. data). All of these band recoveries and relocations are proof that the owls are capable of crossing mountain ranges, and it may be possible that such a southwestern migratory route is used by owls from other regions on the eastern side of the continental divide. The evidence that a Burrowing Owl has the ability to cross a mountain range somewhere between southern Arizona and southern Saskatchewan supports the likelihood of Burrowing Owls dispersing between southern locations such as Nevada and Washington State, and the Great Plains. The band recovery also provides support to the likelihood of owls dispersing the great distances as suggested by SIA, e.g. between southern regions such as those in Arizona, New Mexico, and Texas; and northern regions such as Alberta, Saskatchewan and Montana (Figure 5-5).

INTER-REGIONAL DISPERSAL AND "SHORT-STOPPING"

The second objective of this study was to determine proportion of owls that dispersed and the direction and distance of the dispersal between breeding seasons. While a high proportion of the Burrowing Owl breeding population is comprised of owls originating in the US, the SIA results suggest there is a net loss of Canadian Burrowing Owls that are stopping short of Canada in subsequent summers.

Traditional survival rates based on band returns have range from 14-43% for adult and 5-6% for juvenile Burrowing Owls (Lutz and Plumpton 1999, Hoyt 2001). Return rates vary with the size of the study area (Figure 5-6). The highest rates of return were from the Regina Plain region and are probably associated with the relatively large size of the study area. The Regina Plain study area is approximately 12 200 square kilometres (Todd 2001), whereas the study areas of Colorado and Alberta were 69 and 350 square kilometres respectively (Lutz and Plumpton 1999, J. Schmutz per. Comm.). The study size for this stable-isotope study is the entire northern Great Plains. Therefore, the detection of inter-region movements of owls is not limited by the boundaries of small study areas.

The SIA results suggest that only 6 of 26 (23%) owls sampled in the Grasslands National Park appeared to have returned to the same breeding ground. The isotopically derived return rate of 44% (23 of 52) in Alberta was similar to the band return rate of the Regina Plain. However, the return rate may be inflated because the Alberta collection area comprised of multiple sites that were not statistically separable across an area approximately 8000 sq km. The owls may have returned to Alberta, but there is a high probability that they did not return to the same general area as the year previous. Such short distance dispersals would not be detected until it is possible to discriminate the isotopic differences between regions within Alberta.

Post-breeding or post-fledging dispersal may allow for the investigation of suitable habitat outside of an owl's current breeding location (Broley 1947, Åkesson et al. 1996). Radio-telemetry tracking of juvenile Burrowing Owls indicates that post-fledging dispersal may only be limited to a few kilometres before the commencement of migration (Clayton and Schmutz 1999, Todd 2001). Therefore, it is unlikely that Burrowing Owls use the late summer, pre-migratory period to prospect for future breeding territories similar to other species (Arguedas and Parker 2000, Oro and Pradel 2000, Bayne and Hobson 2001, King and Belthoff 2001).

A more likely reason for high rates of natal and/or breeding dispersal may be vacant suitable habitat along migratory pathways. Waterfowl species such American Wigeon (*Anas Americana*), Green-winged Teal (*A. crecca*), Northern Shoveler (*A. clypeata*), Northern Pintail (*A. acuta*), and Lesser Scaup (*Aythya affinis*) are known to fill their habitat in the order it is encountered during spring migration (Johnson and Grier 1988). The owls may simply halt their spring migration when they arrive at any suitable habitat and go unchallenged by other owls. Radio-telemetry studies of migrating Burrowing Owls have demonstrated that the owls can cover approximately 200 km per night (G. Holroyd unpubl. data). Fall migration can take up to three weeks during September through November and spring migration can last as long as eight weeks during March and April (Haug et al. 1993, G. Holroyd unpubl. data). Compared to other raptors such as Peregrine Falcons that can cover 500 km per day (Holroyd and Duxbury 1999), the owl migration period is relatively long. With low fidelity to breeding locations, the relatively slow spring migration may allow for the exploration for suitable sites. The Arizona-Saskatchewan recapture provides proof that Burrowing Owls from Saskatchewan / Montana may breed as far away as Arizona in a subsequent year.

TRANS-BORDER DISPERSAL AND EXCHANGE

Population models could help prioritize the demographic parameters that need to be addressed to reverse the decline of Burrowing Owls (Holroyd et al. 2001). However, population models that include survival estimates based on return rates will be erroneous (Lebreton et al. 1992, Chase et al. 1997, Wellicome 1997b, Marshall et al. 2000, DiQuinzio et al. 2001, Johnson et al. 2001, Fernandez et al. 2003). As shown earlier, there is an inherent bias associated with the size of study areas. The larger the study area, the greater the chance of recapturing locally marked owls. Even short-distance dispersal would be missed in smaller study areas. The SIA results indicate that Burrowing Owls have low regional fidelity. If return rates are substituted for survival rates, the assumed survival rates would appear to be lower than what they may actually be. Burrowing Owls may survive for multiple years after being marked, but go undetected because they permanently emigrate to other regions. According to the SIA results and the relationship described by Equations 1-3, population models in Canada should incorporate a 22.2% reduction to the post-breeding population. This reduction will account for the number of owls that will emigrate to the US and not be replaced by immigrants from the US.

In a comparison to the effects of productivity on population change found in the Regina Plain, Equation 1 is a close estimate for population change as determined by survey data. Equation 1 predicts that to maintain the Burrowing Owl population of Canada (proportion of population change in a subsequent year = 1.0), each pair would have to produce 6.4 young per nest (Figure 5-7). In the Regina Plain, the relationship between productivity and the percent change in population in a subsequent summer predicts 6.3 young per pair is required to ensure a stable population of Burrowing Owls (Poulin 2003).

DISPERSAL AND HABITAT

A combination of factors such as vegetation composition, habitat fragmentation, climate, prey abundance, and land-use activities has created a complex prairie ecosystem (Peterjohn 2003). The changes in population sizes, dispersal rates and the degree of site fidelity caused by the complexity of grasslands can vary between species and between years (Delisle and Savidge 1997, Davis and Duncan 1999, Murphy 2003).

Drought conditions can reduce the number of viable wetlands (Bethke and Nudds 1995). The dispersal of waterbird and waterfowl species in the "Prairie Pothole" region may be affected by a reduction in wetlands because of a positive correlation between population size and the number of wetlands (Niemuth and Solberg 2003). Piping Plover (*Charadrius melodus*) dispersal patterns are affected by the heterogeneity of suitable habitat being caused by changing climatic conditions (Plissner and Haig 2000).

Changes in land use patterns also affect the dispersal patterns of grassland-nesting birds. In conjunction with a reduction of wetlands, increases in the amount of cropland can alter inter-year settling patterns of habitat-opportunistic species, such as the Northern Pintail. In areas where pintails settle to breed, nest success is negatively correlated with the amount of cropland that is intermixed with suitable habitat (Greenwood et al. 1995). Site fidelity is low for species such as pintails and Blue-winged Teals (*Anas discors*) that seek suitable nesting habitat that has the required quantity of wetlands and relatively low proportions of cropland (Johnson and Grier 1988, Hestbeck 1995, Austin 2002, Podruzny et al. 2002).

Changes in prey abundance across the landscape alter the dispersal and distribution of nomadic predators. Non-philopatric species such as Short-eared Owls (*Asio flammeus*) take advantage of randomly occurring irruptions of prey populations (Holt and Leasure 1993, Poulin et al. 2001). Once a prey population begins to cycle downwards nomadic predators can disperse to take advantage of another prey source (Norrdahl and Korpimaki 1996).

Burrowing Owl Dispersal. The wandering tendencies of Burrowing Owls suggested by the isotope results may have evolved at a time when Prairie Dogs and their colonies ranged across western North America. While not officially listed as an endangered species, the once ubiquitous Prairie Dog is now a disappearing on the Great Plains. It is estimated that only 311,000 hectares of occupied habitat currently exists in fragments range wide; a range that was estimated to be approximately 155.5 million hectares in the late 1800's (USFWS 2001). It follows that such a reduction of Prairie Dogs and their burrows has been deleterious to the quantity and distribution of Burrowing Owls. While perhaps not to the same degree, large expanses of contiguous breeding habitat would have allowed Burrowing Owls to exist in more irruptive patterns similar to other nomadic species such as Short-eared Owls.

Grasshoppers can be an important prey source for Burrowing Owls, especially during the post-fledging period (Haug et al. 1993, Wellicome and Haug 1997). Outbreaks of grasshoppers were dramatic, large and cyclic before they were suppressed as pests and by cultivation of habitat since the end of the 19th century (Schlebecker 1953). Before settlement and pest control, Burrowing Owls may have responded to outbreaks by settling in areas of peak grasshopper densities. Burrowing Owl numerical responses to changes in prey density are asynchronous (Poulin et al. 2001). However, if prehistoric grasshopper outbreaks went unchecked they could have lasted for years (Skinner 2000, Poulin et al. 2001) and Burrowing Owls may have dispersed into areas where outbreaks were occurring. An asynchronous population response caused by increased productivity may have occurred subsequently and lasted until the grasshopper population began to cycle downwards. Once the numbers of grasshoppers could no longer support a growing population of Burrowing Owls, the large expanses of Prairie Dog towns would have allowed the owls to disperse to areas where grasshopper outbreaks were occurring.

Since European settlement, small mammals have benefited from occasional early winters that prevented the harvest of grain crops. Sheltering snow and a bountiful winter food source lead to population irruptions in subsequent summers (Houston et al. 1997). The numerical responses of Burrowing Owls following post-settlement, small-mammal outbreaks indicate that current levels of prey availability are likely lower relative to levels that may have historically sustained larger broods (Poulin et al. 2001). The degeneration of small mammal habitat due to crop conversion and intensive grazing of native grasslands has probably also depressed the frequency and magnitude of small mammal outbreaks (Poulin 2003). Similar to the grasshopper theory presented above, Burrowing Owls with nomadic-like dispersal could have also taken advantage of irruptions that occurred randomly across a landscape of contiguous grasslands.

The diet of a Burrowing Owl probably reflects the most abundant suitable prey source in a given area (Poulin 2003). Pellets and prey remains that reflect a high reliance on small mammals would likely be found in areas were small mammals are readily available. The conversion of native grasslands to cropland has meant the introduction of aggressive grasshopper suppression programs (Skinner 2000). In addition, the replacement of native grasses with grain crops has increased food availability for small mammals, and increased edge habitat. An increase in edge habitat may have made small mammal prey more available for Burrowing owls (Orth and Kennedy 2001). Therefore, a high proportion of small mammal prey in the diet of Burrowing Owls may represent a diet adaptation subsequent to the suppression of grasshoppers. This adaptation may be supported by the domination of grasshopper remains in pellets found at successful nests in a region of a grasshopper outbreak in 2003 (personal observation). The lack of mammalian prey in these pellets suggests Burrowing Owl nestlings can be raised successfully on a diet of only grasshoppers.

It may also be possible that Burrowing Owl dispersal tendencies could have co-evolved with habitat alterations caused by large herds of grazing mammals and/or fire. Before settlement, herds of four million bison (*Bison bison*) were thought to be possible with total estimates of 30 to 75 million bison across the prairies (Seton 1929, Roe 1970, McHugh 1972, Weber 2001). Such grazing pressure would likely produce expanses of suitable habitat with reduced vegetation height. Uncontrolled grassland fires would have inhibited the encroachment of brush and trees to maintain a mosaic of habitats across the grasslands (Briggs et al. 2002). Once the herds moved off or the effects of fire disappeared in subsequent years, the species composition in these areas would have changed. The distribution of Baird's Sparrows (*Ammodramus bairdii*) is negatively correlated with areas with suppressed vegetation height due to intensive grazing pressures (Sutter et al. 1995, Dale et al. 1997, Davis et al. 1999). If Baird's Sparrow nesting habitat is subjected a grassland fire, it takes three years to re-establish their population to pre-fire levels (Pylypec 1991). Grazing and fires would have had an opposite effect on the distribution of Burrowing Owls. If the vegetation height at the nest site is a key factor in suitable Burrowing Owl habitat (Uhmann et al. 2001), nomadic herds of mammals and fire would have provided temporary nesting habitat across the prairies. The ability to disperse long distances would allow the owls to relocate in areas that were more suitable once the suitable effects of grazing and fire are diminished by the succession of less suitable plant species.

Burrowing Owls may have been semi-nomadic before settlement. Contiguous habitat would have provided the owls with the freedom to disperse between colonies that may have developed in response to peaks in prey populations. Their partial site fidelity would have maintained established Burrowing Owl colonies, while their tendency to wander would provide owls to search for newly grazed habitat or new sources of prey. The period of 100 years since settlement is unlikely to have been enough time to adapt to the loss and fragmentation of habitat. Across much of their range, the owls are now restricted to breed on remnants of their former habitat separated by expanses of unsuitable agricultural land. However, their ability to migrate still allows for long distant dispersal.

The factor that ultimately drives dispersal is likely the availability of prey in the remnants of their habitat, and the configuration of what remains of native prairie would play an important role in the patterns and scale of dispersal of Burrowing Owls. If a patch of habitat that contains quality nesting habitat but lacks the food resources required to raise a successful nest, it is probable that Burrowing Owls would not remain in such an area. The owls would be forced to disperse to in search of habitat that can support a breeding attempt. Their weak site fidelity would allow the owls to relocate over large distances in search of areas with suitable prey levels. Perhaps, since Burrowing Owls have a relatively short life span (Haug et al. 1993), their life strategy is about actively finding a good food source instead of depending on local changes. What is not known is the relationship between long distant dispersals and current irruptions of grasshopper populations across the Great Plains.

The introduction of unsuitable habitat between remnants of suitable habitat may be altering dispersal patterns by making populations at the periphery of the owls' range energetically inefficient to maintain. Current estimates indicate that populations in Montana are below carrying capacity (Restani et al. 2001). It is probable that many other populations within the Burrowing Owl range are also below carrying capacity. Vacancies in suitable habitat may have a greater chance of being reoccupied where the expenditure of the least amount of energy for migration would be required.

The population declines and extirpations at the northern and eastern limits of the Burrowing Owl range may be an indication that the peripheral populations are experiencing recruitment difficulties. With an apparent lack of site fidelity coupled with "short-stopping" on spring migrations; there is little wonder that release programs in peripheral populations have been unable to increase local recruitment rates (De Smet 1997, Leupin and Low 2001, D.L. Todd unpublished data).

Extirpated, peripheral Burrowing Owl populations are not being re-colonized. In theory, the survival of metapopulations requires the re-colonization of extinct sub-populations (Plissner and Haig 2002). The persistence of the current range of the western Burrowing Owl depends on the dispersal of individuals from core populations to the extremities of its range to ensure continuity. For re-colonization dispersal to occur, "sub-populations" must have asynchronous population trends so that increasing populations are available to balance decreasing populations (Wiens 1996). Only two regions within the entire range of the western Burrowing Owl have increasing trends as detected by the Breeding Bird Survey; Colorado and southern California (C. Conway pers. comm.). The remaining populations across western North America are stable or decreasing. Canadian population declines due to depressed productivity are compounded by a net loss of Burrowing Owls to the US. If the productivity in populations that provide Canadian populations with foreign recruits decline, the net loss due to dispersal will increase and the declines in Canadian populations will accelerate.

The re-colonization of extinct populations is a key component of metapopulation theory (Plissner and Haig 2002). The lack of re-colonization of areas where Burrowing Owl populations once existed may mean that metapopulation theory may not fit Burrowing Owl population dynamics. However, the large dispersal distances detected by SIA indicate that the development of models within individual populations may not be prudent because the emigration and immigration dynamics occur at a far greater scale than individual populations. Therefore, models should be created at a metapopulation or continental scale to ensure permanent emigration is detected and is separated from rates of survivorship.

High dispersal rates of animals have likely evolved in response to ephemeral habitat availability (Travis and Dytham 1999). The SIA results of this study indicate large-scale dispersal rates for Burrowing Owls. Current Burrowing Owl dispersal rates are potentially related to historical patterns in the configuration and lifespan of suitable nesting and foraging habitat. Post-settlement habitat loss and/or degradation have introduced habitat fragmentation that has added to natural habitat patchiness. Large-scale dispersal of Burrowing Owls may be on the increase in order to adapt to the changing quality of contemporary habitat fragments.

Not only is the quality of suitable fragments important, but also the duration the fragments are available (Keymer et al. 2000). Time will determine the persistence of Burrowing Owls in the fragments, as the characteristics that make habitat suitable are altered over time. If fragments change with time and become too small or inhospitable, the owls will disperse from a fragment to relocate in a more suitable fragment. The success of dispersal will depend on the connectivity of the remnant habitat, especially as habitat availability decreases. Data to investigate spatiotemporal parameters such as patch size, fragmentation, configuration and lifespan of Burrowing Owl habitat at a metapopulation or continental scale is required in addition to demographic information in order to examine the dynamics of the western Burrowing Owl as a whole. In order to accomplish such a considerable task, international collaboration and data collection will be required.

ACKNOWLEDGEMENTS

I would like to thank L. Priestley, and D. Birn for their assistance in the lab. Many thanks go to the feather collectors because without them, this study would not have been possible: G. Holroyd, H. Trefry, D. Shyry, R. Sissons, D. Scobie, R. Russell, J. Nicholson, D. Todd, R. Poulin, P. Bartels, J. Belthoff, R. Griebel, D. Rosenberg, L. Trulio, J. Barclay, P. Delevoryas, G. Proudfoot, G. Batey, N. Korfanta, E. Valdez, C. Conway, J. Everett, M. Robbins, J. Sleno, P. Arrowood, and M.K. Skoruppa. Also, thanks to Environment Canada's Stable-isotope Laboratory for running the C&N analyses. I am grateful of H. Trefry for taking over the permit application process, and MK. Skoruppa for providing the logistical support of organizing and shipping feathers from the US. Special thanks go to G. Holroyd of the Canadian Wildlife Service for his endless logistical and financial support. Special thanks also go to K. Muehlenbachs of the Department of Earth and Atmospheric Sciences at the University of Alberta for his guidance in stable-isotope analysis, and for providing laboratory space and in-kind support. Approval for this project was provided by the Animal Care Committee of the Canadian Wildlife Service. Finally, I am grateful to Environment Canada; the Natural Sciences and Engineering Research Council of Canada; Alberta Sports, Recreation, Parks, and Wildlife Fund; National Fish and Wildlife Fund (US); and the University of Alberta for providing the funding for this project.

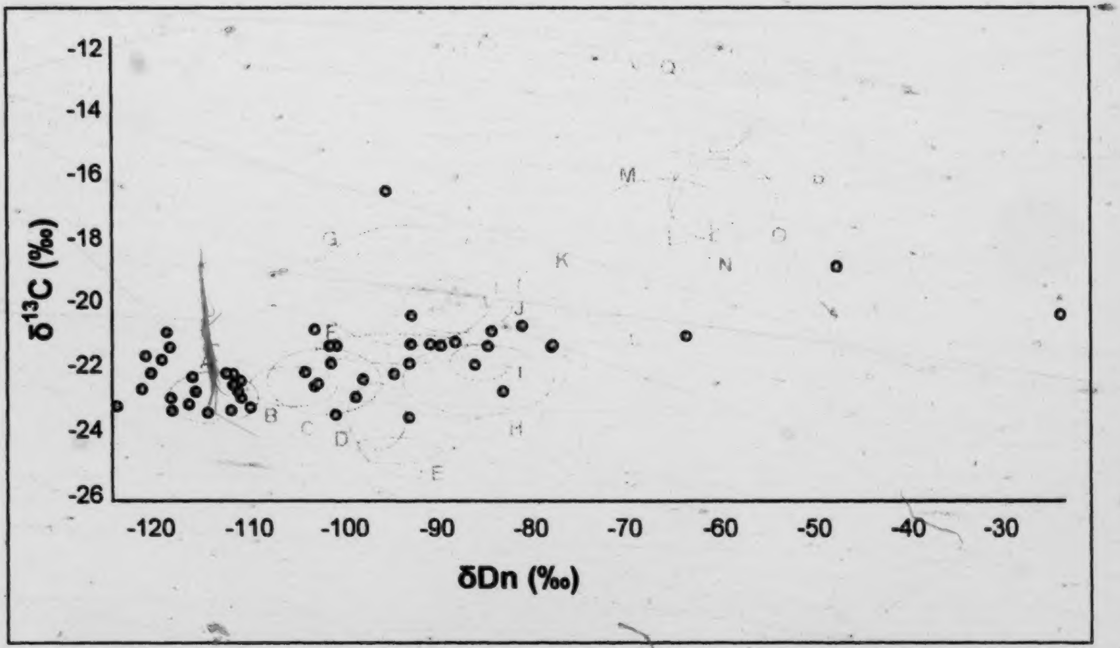


Figure 5-1a. Plots of δD_n and $\delta^{13}C$ values of 52 feathers from after-hatch-year Burrowing Owls captured in Alberta. Ellipses represent areas encircling ± 1 SD of all sample areas within collection areas. See Figure 4-1 for alpha-code representation.

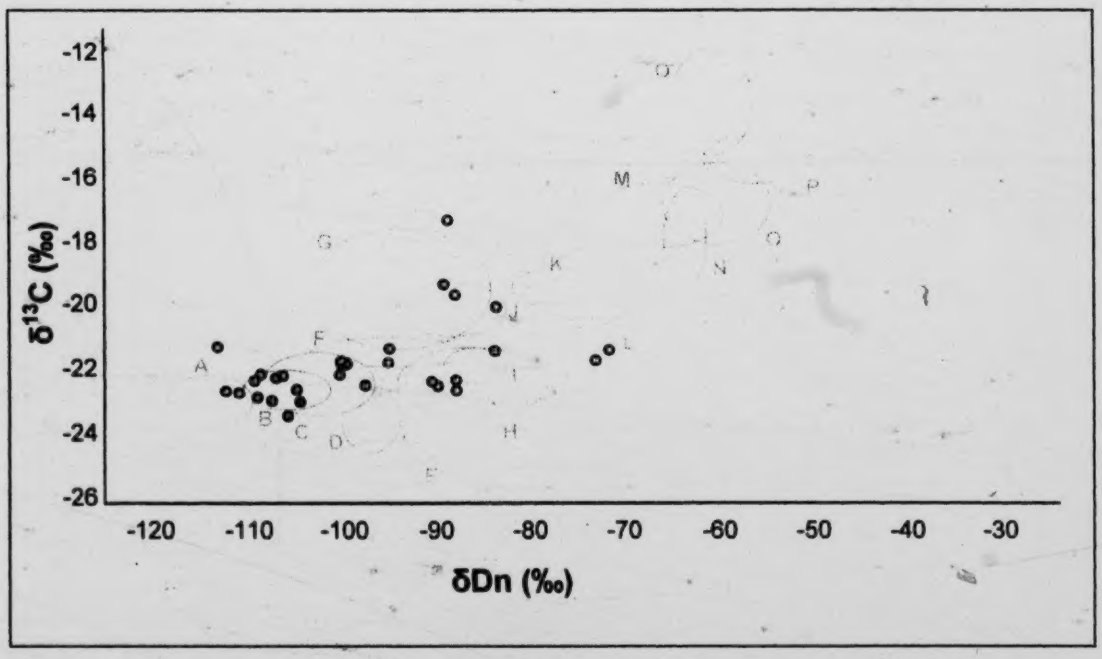


Figure 5-1b. Plots of δD_n and $\delta^{13}C$ values of 32 feathers from after-hatch-year Burrowing Owls captured in Saskatchewan. Ellipses represent areas encircling ± 1 SD of all sample areas within collection areas. See Figure 4-1 for alpha-code representation.

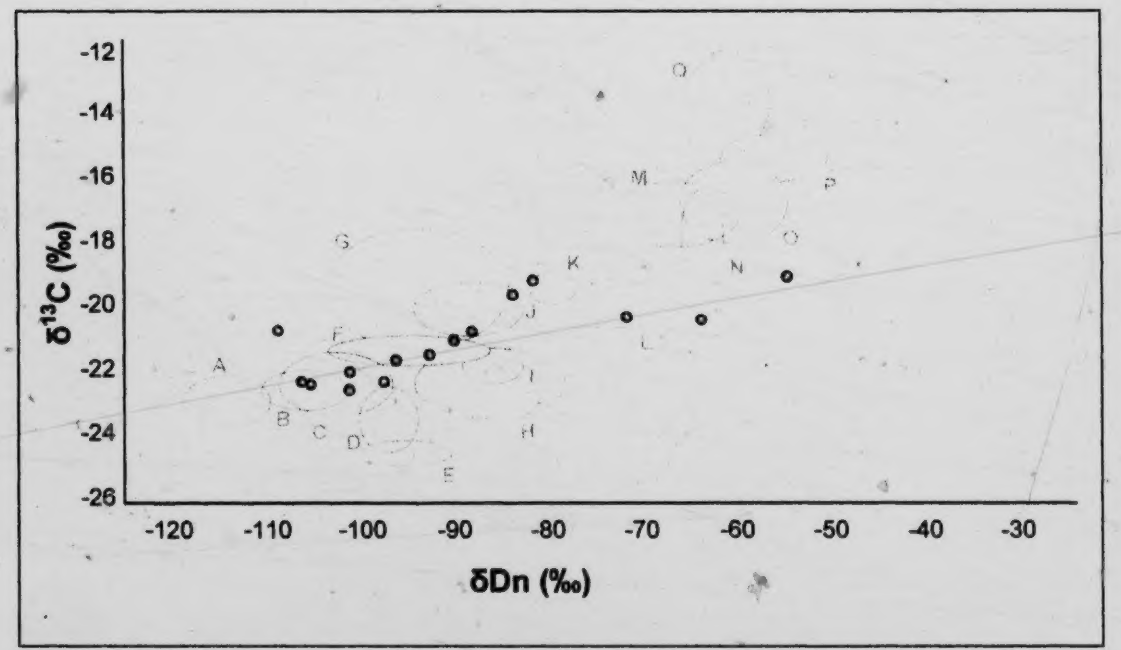


Figure 5-1c. Plots of δD_n and $\delta^{13}C$ values of 15 feathers from after-hatch-year Burrowing Owls captured in the Fort Belknap I.R., Montana. Ellipses represent areas encircling ± 1 SD of all sample areas within collection areas. See Figure 4-1 for alpha-code representation.

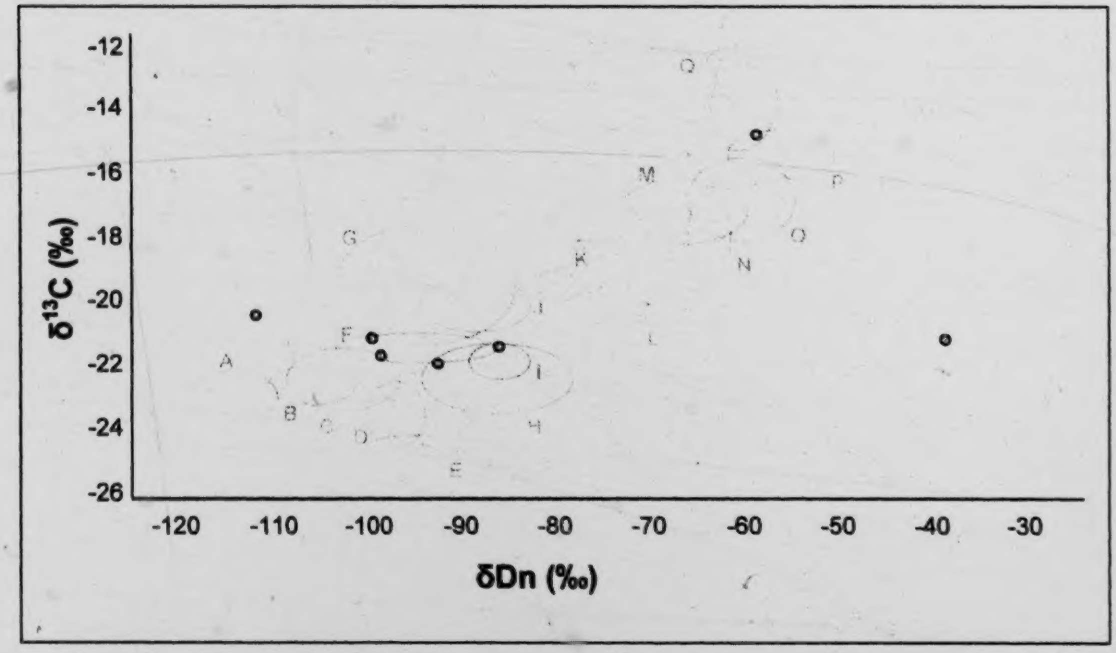


Figure 5-1d. Plots of δD_n and $\delta^{13}C$ values of 7 feathers from after-hatch-year Burrowing Owls captured in Wyoming and North Dakota. Ellipses represent areas encircling ± 1 SD of all sample areas within collection areas. See Figure 4-1 for alpha-code representation.

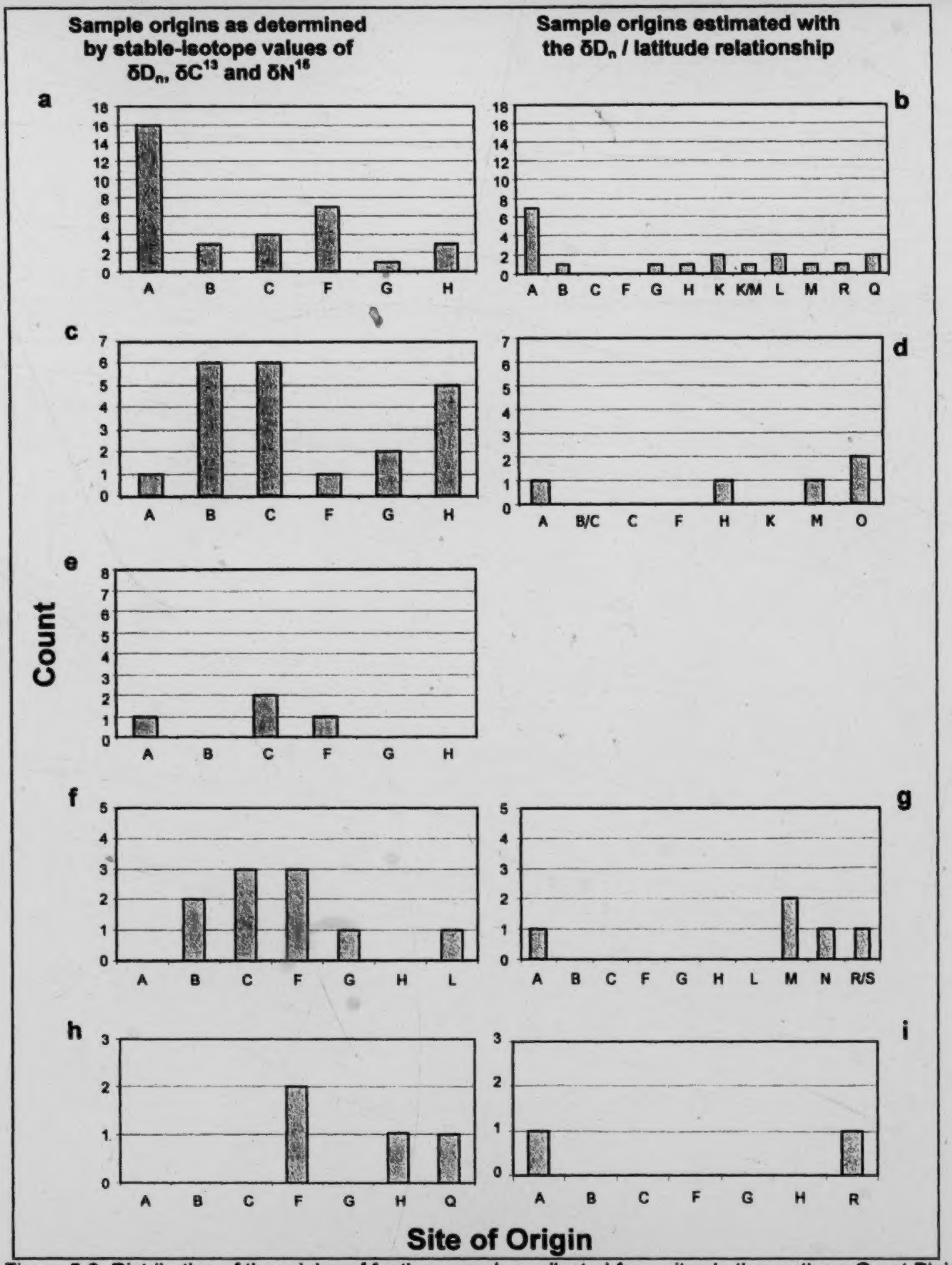


Figure 5-2. Distribution of the origins of feather samples collected from sites in the northern Great Plains (a&b = Alberta; c&d = Grasslands National Park, SK; e = Regina Plain, SK; f&g = Fort Belknap I.R., MT; h&i = Wyoming/North Dakota). The estimated origins of samples that could not be placed by δD_n and $\delta^{13}C$ values were determined by the relationship between δD_n and latitude. See Figure 4-1 for x-axis alpha-code representation. Note the change of scale on the y-axis.

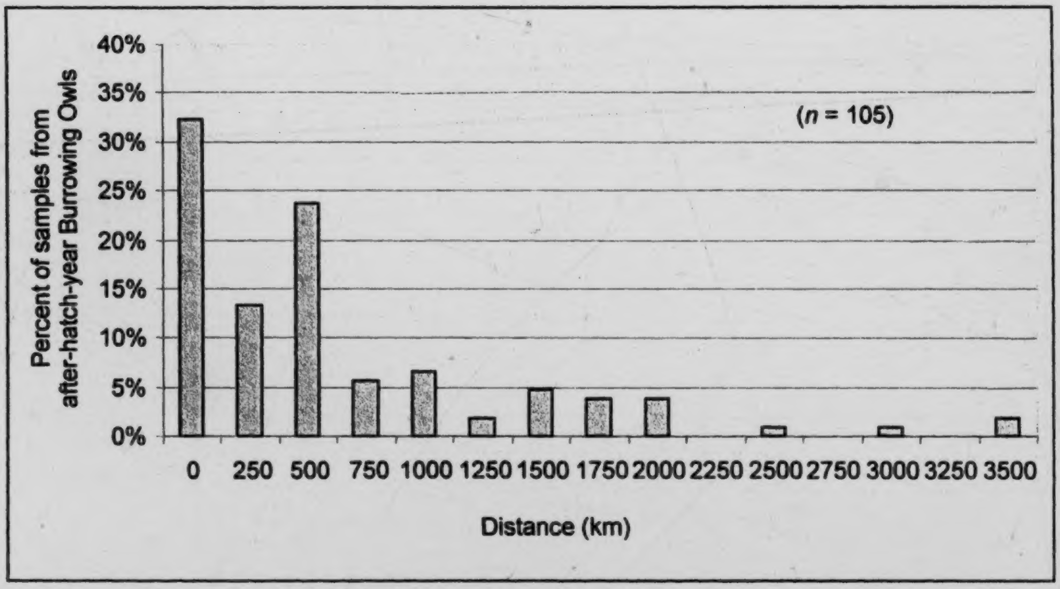


Figure 5-3. Burrowing Owl dispersal distances. Distances between collection areas were placed into gross distance categories by rounding to the nearest 250 km.

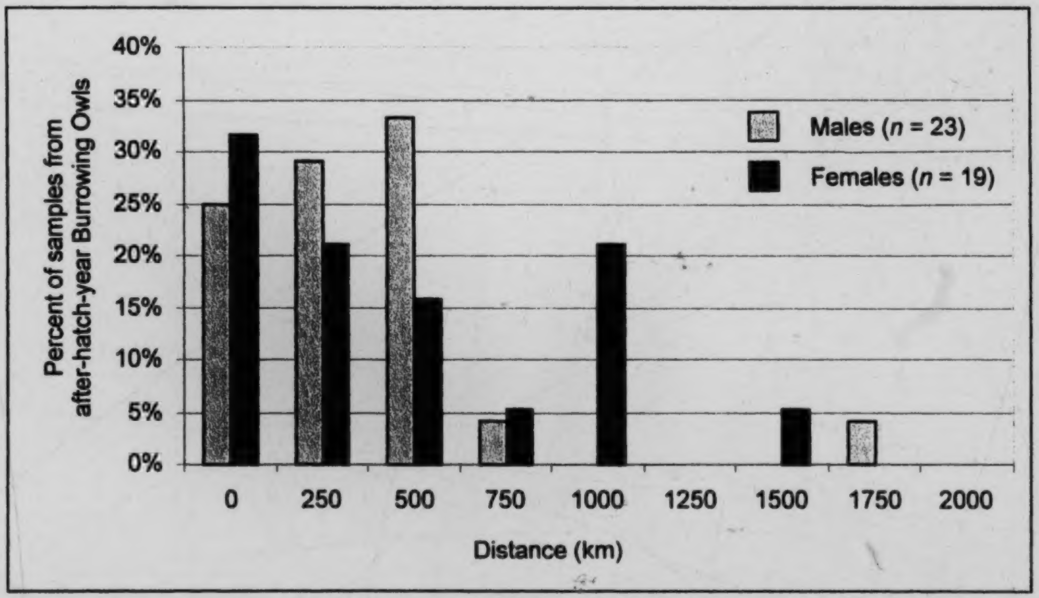


Figure 5-4. The difference in Burrowing Owl dispersal distances by sex. Fifty-two of the 105 after-hatch-year owls were sexed at the time of feather collection. The distance is measured between where the feather sample was collected and the original breeding location the previous year. Distances between collection areas were organized into gross distance categories by rounding to the nearest 250 km.

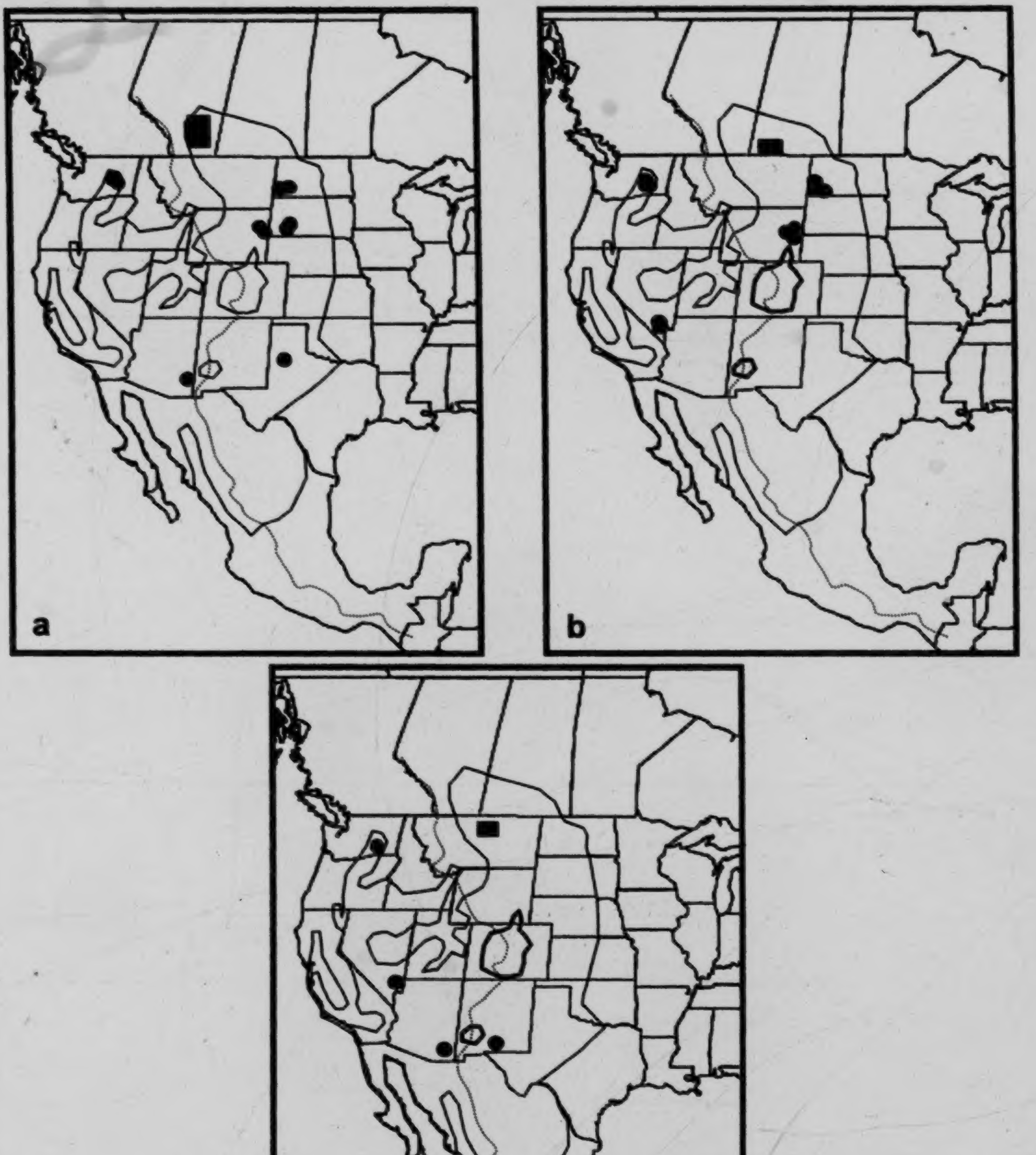


Figure 5-5. Long-distant dispersals: The estimated origins of Burrowing Owl sampled in Alberta (a), Grasslands National Park, Saskatchewan (b), and the Ft. Belknap I.R. in Montana (c). Rectangles represent the collection areas and circles are located in areas where the owls are estimated to have originated the year previous. The large shaded area represents the summer range of the Western Burrowing Owl. The dotted line represents the continental divide.

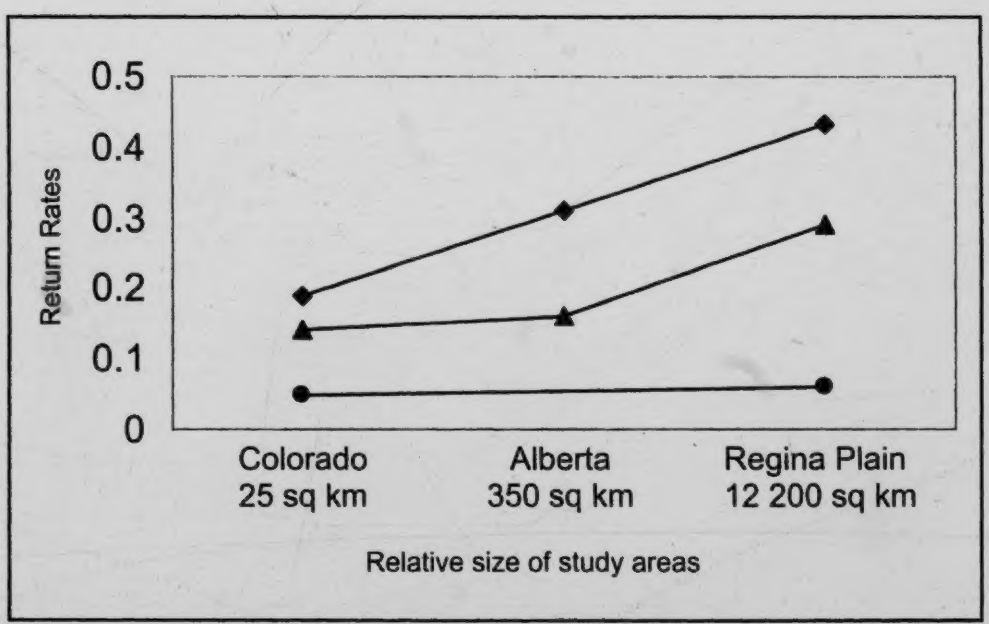


Figure 5-6. The relationship between the return rates of banded Burrowing Owls and the size of the study areas where the recoveries took place. Studies included in the comparison were conducted in Colorado (Lutz and Plumtom 1999), Alberta (Hoyt 2001) and Regina (Hoyt 2001). Rates are provided for after-hatch-year males (diamonds), after-hatch-year females (triangles), and owls banded as juveniles (circles).

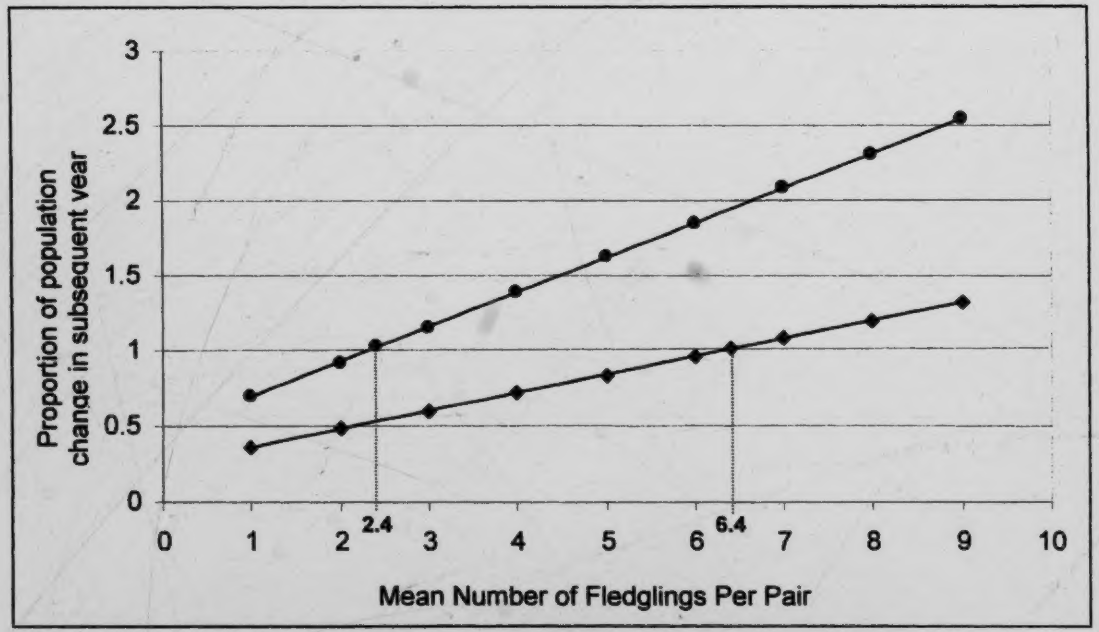


Figure 5-7. Relationship between the number of fledglings produced per pair of Burrowing Owls and the relative size of the breeding population in the subsequent year as predicted by $NY_{+1} = N_R - \Delta E$. With the current net difference between immigration and emigration, the number of Burrowing Owls in Canada would remain stable if each pair fledged 6.4 young (diamonds). If immigration equalled emigration, only 2.4 young per breeding pair would be required for a stable population (circles).

LITERATURE CITED

Åkesson, S., L Karlsson, G. Walinder, and T. Alerstam. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. Behavioral Ecology and Sociobiology 38:293-302.

Araújo, M. B. and P.H. Williams. 2001. The Bias of Complementarity Hotspots toward Marginal Populations. Conservation Biology 15:1710–1720.

Arguedas, N. and P.G. Parker. 2000. Seasonal migration and genetic population structure in House Wrens. Condor 102:517-528.

Arrowood, P.C., C.A Finley, and B.C. Thompson. 2001. Analyses of Burrowing Owl populations in New Mexico. Journal of Raptor Research 35:362-370.

Austin, J.E. 2002. Responses of dabbling ducks to wetland conditions in the Prairie Pothole Region. Waterbirds 25:465-473.

Bayne, E.M. and K.A. Hobson. 2001. Movement patterns of adult male ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. Condor 103:343-351.

Barko, V.A. 1997. History of policies concerning the black-tailed prairie dog: A review. Proceedings of the Oklahoma Academy of Science 77:27-33.

Bethke, R.W. and T.D. Nudds. 1995. Effects of climate change and land use on duck abundance in Canadian prairie-parklands. Ecological Applications 5:588-600.

Blus, L.J. 1996. Effects of pesticides on owls in North America. Journal of Raptor Research 30:198-206.

Briggs, J.M., A.K. Knapp, and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. American Midland Naturalist 147:287-294.

Broley, C.L. 1947. Migration and nesting of Florida bald eagles. Wilson Bulletin 59:3-20.

Burke, D.M. and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications 10:1749-1761.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry, and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecolgia 109:132-141.

Chase, M.K., N. Nur, and G.R. Geupel. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. Auk 114:354–366.

Clayton, K.M. and J.K. Schmutz. 1999. Is the decline of Burrowing Owls *Speotyto cunicularia* in prairie Canada linked to changes in Great Plains ecosystems? Bird Conservation International 9:163–185.

Clayton, K.M. and J.K. Schmutz. 1997. Burrowing (*Speotyto cunicularia*) Owl Survival in Prairie Canada. Pages 107-110 *in* J. Duncan, D.H. Johnson, and T.H. Nicholls [Eds.], Biology and conservation of owls of the northern hemisphere: 2nd international symposium. USDA General Technical Report NC-190, St. Paul, MN USA.

Cormie, A. B., H. P. Schwarcz, and J. Gray. 1994. Relation between hydrogen isotopic ratios of bone collagen and rain. Geochimica et Cosmochimica Acta 58:377–391.

Craig, H. 1953. The geochemistry of stable carbon isotopes. Geochimica Cosmochimica Acta. 3:53-92.

Craig, H. 1954. Carbon-13 in plants and the relationship between carbon-13 and carbon-14 variations in nature. Journal of Geology 62:115-149.

Dale, B.C., P.A. Martin, and P.S. Taylor. 1997. Effects of hay management on grassland songbirds in Saskatchewan. Wildlife Society Bulletin 25:616-626.

Dansgaard, W. 1964. Stable isotopes in precipitation. Tellus 16:436-468.

Davis, S.K. and D.C. Duncan. 1999. Grassland songbird occurrence in native and crested wheatgrass pastures of southern Saskatchewan. Studies in Avian Biology 19:211–218.

Davis, S.K., D.C. Duncan, and M. Skeel. 1999. Distribution and habitat associations of three endemic grassland songbirds in southern Saskatchewan. Wilson Bulletin 111:389-396.

Delisle, J.M., and J.A. Savidge. 1997. Avian use of vegetation characteristics of conservation reserve program fields. Journal of Wildlife Management 61:318-325.

De Smet, K.D. 1997. Burrowing Owl (*Speotyto cunicularia*) monitoring and management activities in Manitoba. Pages 123-130 *in* J. Duncan, D.H.

Johnson, and T.H. Nicholls [Eds.], Biology and conservation of owls of the northern hemisphere: 2nd international symposium. USDA General Technical Report NC-190, St. Paul, MN USA.

Desmond, M.J., J.A. Savidge, and K.M. Eskridge. 2000. Correlations between burrowing owl and black-tailed prairie dog declines: A 7-year analysis. Journal of Wildlife Management 64:1067-1075.

Desmond, M.J. and J.A. Savidge. 1996. Factors influencing burrowing owl (*Speotyto cunicularia*) nest densities and numbers in western Nebraska. American-Midland-Naturalist 136:143-148.

DeNiro M.J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42:495–506

DiQuinzio, D.A.,1 P.W.C. Paton, and W.R. Eddlemann. 2001. Site Fidelity, philopatry, and survival of promiscuous Saltmarsh Sharp-tailed Sparrows in Rhode Island. Auk 118:888–899.

Duxbury, J.M. 1998. An Application of Stable Isotope Ecology to the Study of Raptor Diets. MSc Thesis, University of Alberta, 150pp.

Duxbury, J.M. G.L. Holroyd and K. Muehlenbachs. 2003. Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope-base maps for tracking migratory birds. *Isotopes in* Environmental and Health Studies 39:179-189.

Ehleringer, J.R. and P.W. Rundel. 1989. Stable isotopes: History, Units, and Instrumentation. Pages 1-15 *in* P.W. Rundel, J. R. Ehleringer, and K.A. Nagy [Eds.], Stable Isotopes in Ecological Research. Springer-Verlag, New York.

Fahrig, L. 1999. Forest loss and fragmentation: Which has the greater effect on persistence of forest-dwelling animals? Pages 87-95 *in* J.A. Rochelle, L.A. Lehmann, and J. Wisniewski [Eds.], Forest Fragmentation: Wildlife and Management Implications. Brill Academic Publishers, Leiden, The Netherlands.

Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modelling 105:273-292.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61:603-610.

Fernandez, G., H. de-la-Cueva, N. Warnock, and D.B. Lank. 2003. Apparent survival rates of Western Sandpiper (*Calidris mauri*) wintering in northwest Baja California, Mexico. Auk 120: 55-61.

Fyfe, R.W. 1977. Status of Canadian raptor populations. Canadian Field Naturalist 90:370-375.

Gobeil, J.F. and M.A. Villard. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98:447-458.

Graves, G.R., C.S. Romanek, and A.R. Navarro. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proceedings of the National Academy of Science 99:8096-8100.

Greenwood, R.J., A.B. Sargeant, D.H. Johnson, L.M. Cowardin, and T.L. Shaffer. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. Wildlife Monographs 128.

Haas, C.A., and S.A. Sloane. 1989. Low return rates of migratory Loggerhead Shrikes: winter mortality or low site fidelity? Wilson Bulletin 101:458-460.

Hanski, I.A. 1999. Metapopulation Ecology. Oxford University Press Inc. Oxford, New York, USA.

Hanski, I.A. and M.E. Gilpin. 1997. Metapopulation Biology: ecology, genetics, and evolution. Academic Press. San Diego.

Harrison, S. and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225-232.

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl (*Speotyto cunicularia*). *In:* A. Poole and F. Gill [Eds.], The Birds of North America, No. 61. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hebert, C.E. and L.I. Wassenaar. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. Environmental Science & Technology 35:3482-3487.

Hess, G.R. 1996. Linking extinction to connectivity and habitat destruction in metapopulation models. American Naturalist 148:226-236.

Hestbeck, J.B. 1995. Response of northern pintail breeding populations to drought, 1961-92. Journal of Wildlife Management 59:9-15.

Hjertaas, D., S. Brechtel, K. De Smet, O. Dyer, E.A. Haug, G. Holroyd, P. James, and J. Schmutz. 1995. National Recovery Plan for the Burrowing Owl. Report No. 13. Recovery of Nationally Endangered Wildlife, Ottawa. 51pp.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable-isotopes: a review. Oecologia 120:314-326.

Hobson, K.A. and L.I. Wassenaar. 2001. Isotopic delineation of North American migratory wildlife populations: Loggerhead Shrikes. Ecological Applications 11, 1545-1553.

Hobson, K.A. and L.I. Wassenaar . 1997. Linking breeding and wintering grounds of neotropical migration songbirds using stable isotopic analysis of feathers. Oecologia 109, 142-148.

Holroyd, G.L., R. Rodríguez-Estrella, and S.R. Sheffield. 2001. Conservation of the Burrowing Owls in western North America: issues, challenges and recommendations. Journal of Raptor Research 35:399-407.

Holroyd G.L. and J.M. Duxbury 1999. Travels of Peregrine #5735. Blue Jay 57:146-149.

Holt, D.W. and S.M. Leasure. 1993. Short-eared owl (*Asio flammeus*) *In:* A. Poole and F. Gill [Eds.], The Birds of North America, No. 62. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Houston, C.S. 1997. Banding of *Asio* owls in south-central Saskatchewan. Pages 237-242 *In* J. R. Duncan, D. H. Johnson, and T. H. Nicholls [Eds.], Biology and Conservation of Owls of the Northern Hemisphere. USDA Forest Service General Technical Report NC-190.

Hoyt, J.S. 2001. Survival Estimates for Three Burrowing Owl Populations in Prairie Canada. Canadian Wildlife Service unpublished report. 19 pp.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211.

James, P.C. and R.H.M Espie. 1997. Current status of the Burrowing Owl in North America: an agency survey. Pages 3-5 *in* J.L. Lincer and K. Steenhof [Eds.], The Burrowing Owl, its breeding biology and management including the proceedings of the first international Burrowing Owl symposium. Journal of Raptor Research. Report 9.

James, P.C., T.J. Ethier, and M.K. Toutloff. 1997. Parameters of a declining burrowing owl Population in Saskatchewan. Pages 34-37 *in* J.L. Lincer and K. Steenhof [Eds.], The Burrowing Owl, its breeding biology and management including the proceedings of the first international Burrowing Owl symposium. Journal of Raptor Research. Report 9.

Johnson, D.H. and J.W. Grier. 1988. Determinants of breeding distribution of ducks. Wildlife-Monographs 100.

Johnson, D.H. and L. Igl. 2001. Area requirements of grassland birds: A regional perspective. Auk 118:24-34.

Johnson, O.W. P.L. Bruner, J.J. Rotella, P.M. Johnson, and A.E. Bruner. 2001. Long-term study of apparent survival in Pacific Golden Plovers at a wintering ground on Oahu, Hawaiin Ilsands. Auk 118:342–351.

Jones, Z.F. and C.E. Bock. 2002. Conservation of grassland birds in an urbanizing landscape: a historical perspective. Condor 104:643–651.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. Nature 326:388-390.

Kareiva, P. and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 372:299-302.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216-221.

Keymer, J.E. P.A. Marquet, J.X. Velasco-Hernandez, and S.A. Levin. 2000. Extinction thresholds and metapopulation persistence in dynamic landscapes. American Naturalist 156:478-494.

Kharaka, Y.K. and W.W. Carothers 1980. Oygen and hydrogen isotope geochemistry of deep basin brines. Pages 305-360 *in* P. Fritz and J.C.H. Fontes [Eds.], *Handbook of Environmental Isotope Geochemistry*. Amsterdam.

King, R.A. and J.R. Belthoff. 2001. Post-fledging dispersal of Burrowing Owls in Southwestern Idaho: Characterization of movements and use of satellite burrows. Condor 103:118-126.

Kirk, D. A., and C. Hyslop. 1998. Population status and recent trends in Canadian raptors: a review. Biological Conservation 83:91-118.

Klute, D. S., L. W. Ayers, M. T. Green, W. H. Howe, S. L. Jones, J. A. Shaffer, S. R. Sheffield, and T. S. Zimmerman. 2003. Status Assessment and Conservation Plan for the Western Burrowing Owl in the United States.

U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication FWS/BTP-R6001-2003, Washington, D.C. 108 pp.

Koenig, W.D., P.N. Hooge, M.T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. Condor 102:492-502.

Koenig, W.D., D. Van Vuren, and P.N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11:514-517.

Korfanta, N.M., L.W. Ayers, S.H. Anderson, and D.B. McDonald. 2001. A preliminary assessment of Burrowing Owl status in Wyoming. Journal of Raptor Research 35:337-343.

Körner, C., F.D. Farquhar, and S.C.Wong. 1991. Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia 88:30-40.

Kyle, C.J. and C. Strobeck 2002. Connectivity of peripheral and core populations of American Wolverines. Journal of Mammalogy 83:1141–1150

Lajtha, K. and J.D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. Pages 1-21 *in* K. Lajtha and R.H. Michener [Eds.], Stable-isotopes in ecology and environmental science. Blackwell, Oxford.

Lebreton, J.D, K.P. Burnham, J. Clobert, and D.R. Aanderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

Leupin, E.E. and D.J. Low. 2001. Burrowing Owl reintroduction efforts in the Thompson-Nicola region of British Columbia. Journal of Raptor Research 35:392-398.

Levins, R. 1970. Extinction. Page 77-107 *in* M. Gerstenhaber, *Ed.* Some Mathematical Questions in Biology. Lecture on Mathematics in the Life Sciences. Vol. 2. American Mathematical Society, Providence, Rhode Island, USA.

Lutz, R.S. and D. L. Plumpton 1999. Philopatry and nest-site reuse by burrowing owls: implications for productivity. Journal of Raptor Research 33:149-153.

Marshall, M.R., R.R. Wilson, and R.J. Cooper. 2000. Estimating survival of neotropical-nearctic migratory birds: are they dead to just dispersed? Pages 195-199 *In*: R. Bonney, D. N. Pashley, R. J. Cooper, L. Niles eds. 2000. Strategies for bird conservation: The Partners in Flight planning process; Proceedings of the 3rd Partners in Flight Workshop; 1995

October 1-5; Cape May, NJ. Proceedings RMRS-P-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Martell, M.S., J. Schladweiler, and F. Cuthbert. 2001. Status and attempted reintroduction of Burrowing Owls in Minnesota, U.S.A. Journal of Raptor Research 35:392-398.

Martin, K., P.B. Stacey, and C.E. Braun. 2000. Recruitment, dispersal and demographic rescue in spatially-structured White-tailed Ptarmigan populations. Condor 102:503-516.

McGarigal, K. and W.C. McComb 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs 65:235-260.

McHugh, T. 1972. The time of the buffalo. A.A. Knopf, New York. 339 pp.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby, and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen. Oecologia 105:53-63.

Mönkkönen, M. and P. Reunanen. 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos 84:302-305.

Muehlenbachs, K. 1986. Alteration of the oceanic crust and the ^{18}O history of seawater. Pages 425-444*in* J.W. Valley, H.P. Taylor, H. P., Jr., and J.R. O'Neil [Eds.], Stable isotopes in high temperature geological processes: Reviews in Mineralogy: Chelsea, Mineralogical Society of America.

Murphy, M.T. 2003. Avian population trends within the evolving agricultural landscape of the eastern and central United States. Auk 120:20–34.

Murphy, R.K., K.W. Hasselblad, C.D. Grondahl, J.G. Sidle, R.E. Martin, and D.W. Freed. 2001. Status of the Burrowing Owl in North Dakota. Journal of Raptor Research 35:322-330.

Niemuth, N.D and J.W. Solberg. 2003. Response of waterbirds to number of wetlands in the Prairie Pothole Region of North Dakota, U.S.A. Waterbirds 26:233-238.

Norrdahl, K. and E. Korpimaki. 1996. Do nomadic avian predators synchronize population fluctuations of small mammals? A field experiment. Oecologia 107:478-483.

Oro, D. and R. Pradel. 2000. Determinants of local recruitment in a growing colony of Audouin's gull. Journal of Animal Ecology 69:106-118.

Orth, P.B. and P.L. Kennedy. 2001. Do land-use patterns influence nest-site selection by burrowing owls (*Athene cunicularia hypugaea*) in northeastern Colorado? Canadian Journal of Zoology. 79:1038-1045.

Park, R. and S, Epstein. 1960. Carbon isotope fractionation during photosynthesis. Geochimica Cosmochimica Acta. 21:110-126.

Peterjohn, B.G. 2003. Agricultural Landscapes: can they support healthy bird populations as well as farm products? Auk 120:14-19.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics. 18:293-320.

Plissner, J.H. and S.M. Haig. 2000. Viability of piping plover *Charadrius melodus* metapopulations. Biological Conservation 92:163-173.

Plumpton, D. L., and R. S. Lutz. 1993. Prey selection and food habits of Burrowing Owls in Colorado. Great Basin Naturalist 53:299-304.

Poulin, R.G. 2003. Relationships between Burrowing Owls (Athene cunicularia), small mammals, and agriculture. PhD Thesis, University of Regina, 145 pp

Poulin, R.G., T.I. Wellicome, and L.D. Todd. 2001. Synchronous and delayed numerical response of a predatory bird community to a vole outbreak on the Canadian prairies. Journal of Raptor Research 35:288-295.

Podruzny, K.M., J.H. DeVries, L.M. Armstrong, and J.J. Rotella. 2002. Long-term response of northern pintails to changes in wetlands and agriculture in the Canadian Prairie Pothole Region. Journal of Wildlife Management 66:993-1010.

Pylypec, B. 1991. Impacts of fire on bird populations in a fescue prairie. Canadian Field Naturalist. 105:346-349.

Restani, M., L.R. Rau, and D. L. Flath. 2001. Nesting ecology of Burrowing Owls occupying Black-tailed Prairie Dog towns in southeastern Montana. Journal of Raptor Research 35:296-303.

Roach, J.L., P. Stapp, B. Van Horne, and M.F. Antolin. 2001. Genetic structure of a metapopulation of Black-tailed Prairie Dogs. Journal of Mammalogy 82:946-959.

Roe, F. 1970. The North American buffalo: a critical study of the species in its wild state (2nd edit) Univ. Toronto Press, 991 pp.

Roslin, T. 2002. Who said that size is all that matters? Trends in Ecology and Evolution 17:10-11.

Rubenstein, D.R., C.P. Chamberlain, R.T. Holmes, M.P. Ayres, J.R. Waldbauer, G.R. Graves, and N.C.Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. Science 295:1062-1065.

Samson, F. B. and F. L. Knopf. 1994. Prairie conservation in North America. BioScience 44:418-421.

Sauer, J. R., J. E. Hines, and J. Fallon. 2003. The North American Breeding Bird Survey, Results and Analysis 1966 - 2002. Version 2003.1, USGS Patuxent Wildlife Research Center, Laurel, MD

Shearer, G., D.H. Kohl, and S.-H. Chien. 1978. The nitrogen-15 abundance in a wide variety of soils. Soil Science Society of America Journal 42:899-902.

Schiegal, W.E. 1972. Deuterium content of peat as a paleoclimatic recorder. Science 175:512-513.

Schimmelmann, A. 1991. Determination of the concentration and stable isotopic composition of nonexchangeable hydrogen in organic matter. Analytical Chemistry 63:2356-2459.

Schlebecker, J. T. 1953. Grasshoppers in American agricultural history. Agricultural History 27:85-93.

Schmutz, J.K. 1997. Selected microhabitat variables near nests of Burrowing Owls compared to unoccupied sites in Alberta. Pages 80-83 *in* J.L. Lincer and K. Steenhof [Eds.], The Burrowing Owl, its breeding biology and management including the proceedings of the first international Burrowing Owl symposium. Journal of Raptor Research. Report 9.

Schulze, E.D., F.S. Chapin, III, and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406-412.

Seton, E.T. 1929. The lives of game animals (4 vols). Doubleday, Doran and Co. Garden City, NJ.

Sheffield, S.R. 1997. Current status, distribution, and conservation of the Burrowing Owl (Speotyto cunicularia) in midwestern and western North

America. Pages 399-407 *in* J. Duncan, D.H. Johnson, and T.H. Nicholls [Eds.], Biology and conservation of owls of the northern hemisphere: 2nd international symposium. USDA General Technical Report NC-190, St. Paul, MN USA.

Sheffield, S.R. and M. Howery. 2001. Current status, distribution and conservation of the Burrowing Owl in Oklahoma. Journal of Raptor Research 35:351-356.

Sheppard, S.M.F. 1986. Characterization and isotopic variations in natural waters. Pages165-177 *in* J.W. Valley, H.P. Taylor, and J.R. O'Neil [Eds.], Reviews in Mineralogy Vol. 16:Stable-isotopes in High Temperature Geological Processes. Mineralogical Society of America, BookCrafters Inc., Chelsea, MI.

Shyry, D.T., T.I. Wellicome, J.K. Schmutz, G.L. Erickson, D.L.Scobie, R.F. Russell, and R.G. Martin. 2001. Burrowing Owl population-trend surveys in southern Alberta:1991-2000. Journal of Raptor Research 35:310-315.

Sidle, J.G., M. Ball, T. Byer, J.J. Chynoweth, G. Foli, R. Hodorff, G. Moravek, R. Peterson, and D.N. Svingen. 2001. Occurrence of Burrowing Owls in Black-tailed Prairie Dog colonies on Great Plains National Grasslands. Journal of Raptor Research 35:316-321.

Sillet, T.S. and R.T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296-308.

Sissons, R., K. Scalise, and T. I. Wellicome. 1998. Nocturnal foraging and habitat use by male Burrowing Owls in a heavily cultivated region of southern Saskatchewan. Journal of Raptor Research 35:304-309.

Skeel, M.A., J. Keith, and C.S. Palaschuk. 2001. A population decline recorded by Operation Burrowing Owl in Saskatchewan. Journal of Raptor Research 35:399-407.

Skinner, K.M. 2000. The past, present, and future of rangeland grasshopper management. Rangeland 22:24-28.

Smith, B.N. and S. Epstein. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. Plant Physiology 47:380-384.

Sternberg, L.S.L. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. Pages 124-141 *in* P.W. Rundel, J. R. Ehleringer, and K.A. Nagy [Eds.], Stable Isotopes in Ecological Research. Springer-Verlag, New York.

Sutherland, G.D., A.S. Harestad, K. Price, and K.P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and animals. Conservation Ecology 4(1): 16. [online] URL:http://www.consecol.org/vol4/iss1/art16.

Sutter, G.C., T. Troupe, and M. Forbes. 1995. Abundance of Baird's sparrows, *Ammodramus bairdii*, in native prairie and introduced vegetation. Ecoscience 2:344-348.

Todd, L. D. 2001. Dispersal and post-fledging mortality of juvenile Burrowing Owls in Saskatchewan. Journal of Raptor Research 35:282-287.

Travis, J. M., and C. Dytham. 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings of the Royal Society of London B, Biological Sciences 266:723–728.

Trzcinski, M. K., L. Fahrig, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications 9:586-593.

Uhmann, T.V., N.C. Kenkel, and R.K. Baydack. 2001. Development of a habitat suitability index model for Burrowing Owls in the eastern Canadian Prairies. Journal of Raptor Research 35:378-384.

USFWS (United States Fish and Wildlife Service). 2001. 12 Month Status Review of the Black-tailed Prairie Dog. [online] URL: http://mountain-prairie.fws.gov/btprairiedog/

Vandermeer, J. and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. American Naturalist 158:211-220.

Van der Merwe, N.J., J.A. Lee-Throp, J.F. Thackeray, A. Hall-Martin, F.J. Kruger, H. Coetzee, R.H. Bell, and M. Lindeque. 1990. Source-area determination of elephant ivory by isotopic analysis. Nature 346:744-746.

VerCauteren, T.L., S.W. Gillihan and S. W. Hutchings. 2001. Distribution of Burrowing Owls on public and private lands in Colorado. Journal of Raptor Research 35:357-361.

Vickery, P.D., and J.R. Herkert. 2001. Recent advances in grassland bird research: where do we go from here? Auk 118:11-15.

Villard, M-A., M.K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13:774-783.

Vogel, J.C., B. Eglinton, and J.M. Auret. 1990. Isotope fingerprints in elephant bond and ivory. Nature 346:747-749.

Walters, J.R. 2000. Dispersal behavior: an ornithological frontier. Condor 102:479-481.

Warnock, R. G., and P. C. James. 1997. Habitat fragmentation and Burrowing Owls (*Speotyto cunicularia*) in Saskatchewan. Pages 477-486 *in* J. Duncan, D.H. Johnson, and T.H. Nicholls [Eds.], Biology and conservation of owls of the northern hemisphere: 2nd international symposium. USDA General Technical Report NC-190, St. Paul, MN USA.

Wassenaar, L.I. and K.A. Hobson. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: New isotopic evidence. Proceedings of the National Academy of the Sciences USA 95:15436-15439.

Wassenaar, L.I. and K.A. Hobson. 2000. Evaluating the use of stable-carbon (δ^{13}C) and H (δD) isotope ratios in feathers to infer breeding origins of Red-winged Blackbirds. Ecological Applications 10:911-916.

Wassenaar, L.I. and K.A. Hobson 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. Environmental Science and Technology 35:1845-1850.

Weber, K.T. 2001. Historic Bison Populations: A GIS-Based Estimate. Proceedings of the 2001 Intermountain GIS Users' Conference, Northern Rockies Chapter of URISA in Boise, ID pp. 45-51.

Wellicome, T.I. 1997a. Reproductive performance of Burrowing Owls (*Speotyto cunicularia*): effects of supplemental food. Pages 68-73 *in* J.L. Lincer and K. Steenhof [Eds.], The Burrowing Owl, its breeding biology and management including the proceedings of the first international Burrowing Owl symposium. Journal of Raptor Research. Report 9.

Wellicome, T. I. 1997b. Status of the Burrowing Owl (*Speotyto cunicularia hypugaea*) in Alberta. Alberta Environmental Protection, Wildlife Management Division, Wildlife Status Report No. 11, Edmonton, AB. 21 pp.

Wellicome, T.I. 2000. The effects of food on reproduction in Burrowing Owls (*Athene cunicularia*) during three stages of the breeding season. Ph.D. dissertation, University of Alberta, Edmonton, AB Canada.

Wellicome, T. I. and E. A. Haug. 1995. Second update of status report on the Burrowing Owl, *Speotyto cunicularia*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario. 32 pp.

Wellicome, T.I., G.L. Holroyd, K. Scalise, and E.R. Wiltse. 1997. The effects of predator exclusion and food supplementation on Burrowing Owl (*Speotyto cunicularia*) population change in Saskatchewan. Pages 487-497 *in* J. Duncan, D.H. Johnson, and T.H. Nicholls [Eds.], Biology and conservation of owls of the northern hemisphere: 2nd international symposium. USDA General Technical Report NC-190, St. Paul, MN USA.

Wellicome, T.I. and G.L. Holroyd. 2001. The second international Burrowing Owl symposium: background and context. Journal of Raptor Research 35:269-273.

Wickman, F.E. 1952. Variations in the relative abundance of the carbon isotopes in plants. Geochimica Cosmochimica Acta. 2:636-639.

Wiens, J.A. 1994. Habitat fragmentation: island *v* landscape perspectives on bird conservation. Ibis 137:S97-S104.

Wiens, J.A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management. pp53-84 in D. R. McCullough, ed. Metapopulations and Wildlife Conservation. Island Press, Covelo, CA.

With, K.A. 1997. The application of neutral landscape models in conservation biology. Conservation Biology 11:1069-1080.

With, K.A. 1999. Is landscape connectivity necessary and sufficient for wildlife management? Pages 97-115 *in* J.A. Rochelle, L.A. Lehmann, and J. Wisniewski [Eds.], Forest Fragmentation: Wildlife and Management Implications. Brill Academic Publishers, Leiden, The Netherlands.

Wuerthner, G. 1997. Viewpoint: the black-tailed prairie dog - headed for extinction? Journal of Range Management 50:459-466.

Chapter 6

Discussion and conclusions

Successful conservation of migratory animals requires knowledge of their year round ecological requirements. The time birds spend on wintering grounds and *en route* to and from their breeding grounds equates to over one half of their annual cycle for most species and likely two-thirds for Burrowing Owls. Breeding success during the summer may be the most crucial factor in the persistence of populations, but the return of breeding adults and the recruitment of offspring are inherently linked to the survival during migrations and the winter. Without knowledge of where and when migrants travel or disperse, conservation efforts can only be focussed on part of their annual requirements.

Stable-isotope analysis (SIA) is a practical tool that has advantages and disadvantages compared to traditional methods of bird migration research. SIA does not rely on previously banded birds to determine the general origin of migrants. Because birds do not need to be banded to be tracked, it is unnecessary to travel to regions to band birds, resulting in substantial cost savings. However, band recoveries have the advantage of making unequivocal links between the locations of banding and recovery. The precision of satellite tracking cannot be matched by any other current technique, as the exact location of a bird can be determined during migration and on the wintering grounds. One drawback is that contemporary battery technology limits the size of transmitters and birds the size of Burrowing Owls are currently too small to have transmitters attached to them. Another drawback of satellite tracking is the expense of the technology resulting in only a few birds tracked per year. Therefore, the overall advantage of SIA is that migration patterns can be determined in a few years instead of decades, as is normally required with a dependence on band recoveries or satellite tracking.

Summary of Results

The first step in this project was to determine what natal feathers should be used to create the isotope reference datasets. Similar to other bird species, Peregrine Falcons are known to utilize endogenous nutrients in the formation of eggs. The plumage stage that reflected the signature of hydrogen isotope ratios indicative of local food sources was unknown. With the use of diet switching experiments with Japanese Quail and captive-bred Peregrine Falcons, the first set of down feathers of hatchlings was found to reflect the stable-isotope values of adult females. For Peregrine Falcons, a significant difference in hydrogen isotope values between the natal down and the juvenile down was observed. There was a further change between the juvenile down and the juvenile body feathers, although this difference was moderate. Precocial Japanese Quail do not have three plumage stages and hatch covered in their juvenile down. There was a significant shift in hydrogen isotope values between the two plumage stages of juvenile down and body feathers, although the isotopic signature of the juvenile plumage did not wholly reflect that of the new diet.

Based on the results of the diet switch experiment, the analysis of Peregrine Falcon, juvenile down was acceptable for the creation of the reference dataset. The use of juvenile body feathers was ideal. Because nest visitations to Peregrine Falcon nests can be limited, the age of nestlings can be variable and limit the choice of what feathers are collected. Natal down should be avoided in the SIA of Peregrine Falcons and likely other altricial species.

The second chapter was an investigation of the migratory origins of fall passage Peregrine Falcons trapped on the Gulf Coast of Texas. Most of the Arctic populations of Peregrine Falcons have had a reduction in the banding and survey effort since their recovery. Some regions are no longer visited. As mentioned above, SIA does not depend on birds to be previously banded. The stable-isotope ratios of hydrogen, carbon and nitrogen in feathers collected from migrating Peregrine Falcons were compared to a reference dataset created from collection sites across northern North America. The results indicated that the majority of the falcons trapped on Padre Island, Texas originated from regions in the northwest Arctic; areas with Peregrine Falcons that are expensive to monitor in the summer. The conclusion of the study was that SIA could help determine which regions of the continent the bird migration station was monitoring. In the future, SIA could play an important role for remotely monitoring regional trends, especially in areas that are no longer rigorously monitored in the summer.

The focus of the dissertation then switched from Peregrine Falcons to Burrowing Owls. Far less is known about the migratory routes and wintering grounds of the owls as compared to the falcons. The locations of wintering grounds for Burrowing Owls breeding in Canada were recently discovered. The link between owls that summer in Canada and winter in Texas and Mexico was made by band recovery and radio-telemetry relocations. SIA was used to determine the proportions of wintering owls that came from various portions of their summer range without the use of bands or transmitters. The stable-isotope ratios of hydrogen, carbon and nitrogen in feathers collected from wintering Burrowing Owls (or from their roosts) were compared to a reference dataset created from natal feathers from collection sites across western North America. Five more links were made between owls that had bred in Canada and subsequently migrated to central Mexico. Another link was made between an owl wintering in Texas and a region of southern Alberta. Overall, the majority of the wintering Burrowing Owls were found to have made a relatively short migration. Most of the owls wintering in central Mexico seemed to have migrated from the southern US or northern Mexico. When body feathers were compared against flight feathers, relatively more body feathers had stable-isotope values similar to Burrowing Owl wintering grounds.

Finally, SIA was used to investigate inter-year, large-scale dispersal dynamics of Burrowing Owls in the Northern Great Plains. SIA of Burrowing Owl feathers was used to determine the regularity of long-distant dispersal, and to determine the proportions and direction of inter-regional dispersal, especially between Canada and the US. Results indicated that many Burrowing Owls probably relocate >500 km between breeding seasons. Dispersal between regions in Canada and the adjacent US states is leading to a net loss of Burrowing Owls from Canada to the US. "Short-stopping" migrations may be related to vacant suitable habitat in areas along migratory pathways. New knowledge of the scope and frequency of dispersal will be valuable to the development of large-scale Burrowing Owl population models that require the separation of winter mortality and permanent emigration.

This study is unique as a reference dataset was created for two species at a continental scale. The datasets of the Peregrine Falcon and Burrowing Owl overlap at three locations (south-central Alberta, Regina, and Kansas) and are close in a fourth (Minnesota / South Dakota). Comparisons for a 1:1 relationship between the δD_n, $\delta^{13}C$ and $\delta^{15}N$ values of both bird species resulted in mixed results (Figure 6-1). Carbon was the least variable and the $\delta^{13}C$ values of both species were very similar at each location ($P<0.001$, $R^2=1.0$; Figure 6-1b). Nitrogen isotope ratio values were the least similar at each location ($P<0.41$, $R^2=0.35$; Figure 6-1c). Hydrogen isotope ratio values were similar for south-central Alberta and Regina, but differed by 10-30 ‰ at the other locations. The similar values in $\delta^{13}C$ values are predictable as the range across North American gradient is relatively small. (Tables 3-2, 4-2). The range within a geographical subset would be predicted to have low variability. Nitrogen isotope ratio values can be greatly altered depending on the number of trophic levels in a food web (Minagawa and Wada 1984, Fry 1988, Hobson and Welch 1992, Hobson 1993). Peregrine Falcons consume a wide variety of prey that are located in various trophic levels and habitats such as piscivorous gulls, insectivorous woodpeckers, and herbivorous ducks (Erickson et al. 1988). However, the diet of Burrowing Owls is dominated by prey that are first-level trophic feeders such as herbivorous small mammals and insects (Haug et al. 1993). Greater diet variability in Peregrine Falcons may also be the reason why their isotope ratio values were more variable than those of the Burrowing Owls (Tables 3-2 and 4-2).

Future Research

The success of these initial studies begs for future feather sampling. If the collection of Peregrine Falcon feathers continues on Padre Island, yearly changes in the Arctic populations of Peregrines can be monitored. The collection of natal feathers on the east and west coasts and southern interior of North America are required for a more complete, continental reference dataset. Feathers should be collected from migrants at other banding stations during fall migrations. The analysis of feathers from across North America would assist stable-isotope migration tracking along migration routes other than the Texas Gulf Coast and help determine the relative proportion falcons from different regions that use each route.

The search for more Burrowing Owl wintering grounds continues in Mexico. If band recoveries continue to be a rarity, feather collections from wintering owls in Mexico that may be Canadian bred are required to establish more links between Mexico and Canada. Since the majority of the feathers collected in central Mexico thus far appear to have been grown in the southern US and northern Mexico, the possibility of a leap from migration needs to be investigated. Wintering locations south of areas in Mexico where samples have been collected, need to be sampled. Also, the moult patterns of different body feather tracts need to be described. If there are body feathers that are consistently replaced on the wintering grounds, they could be collected during the breeding season and be used to track the owl back to where it wintered. If this is possible, the complete annual cycle of an owl can be described with the collection of two feathers. The body feather could indicate where the owl spent the winter and a flight feather would indicate the location of where the owl was the previous summer. Including the capture, one would know the location of a given owl at three different times, but only need to hassle the owl once. With mark-recapture, an owl would have to be captured and then subsequently approached twice more to get similar information.

The determination of large-scale dispersal patterns of Burrowing Owls is the first step towards an understanding of the relationship between the owls and what remains of its habitat. The combination of SIA analyses, band return data and digitized landscape attributes will aid in the attempt to connect dispersal with the characteristics of remnant habitat. Over time, an examination of the relationship between dispersal patterns and landscape attributes will lead towards an understanding of the possible effects of landscape loss, alteration, fragmentation and configuration at a multi-regional scale. Currently, we do not know the extent of dispersal patterns of regions south of the northern Great Plains. The proportions of inter-regional dispersal among the central and southern states of the U.S. will lead to a better understanding of the prevalence of "short-stopping" along the migratory route of the Burrowing Owl. The inclusion of samples from the west coast will help determine continental-scale dispersal patterns. These very large-scale dispersal patterns will provide key information for the possible creation of continental-scale models for the entire range of the western Burrowing Owl.

For dispersal patterns and models to be more informative, the development of a technique to distinguish one-year-old Burrowing Owls from those older than one year is necessary to distinguish differences in the patterns and scale of natal and breeding dispersal. Such a technique needs to be used by anyone collecting feathers for isotope analysis.

One of the main concerns in stable-isotope tracking is the lack of consistency in the reporting of data between studies (Hobson 2002). There seems to be mixed opinions about the impact of exchangeability of hydrogen has on data. There are some exciting results stemming from the use of SIA to investigate migratory birds, but the results lack consistency due to the use of different equilibration techniques (see Meehan *et al.* 2001, Hobson *et al.* 2001, Kelly *et al.* 2002, Rubenstein *et al.* 2002). There is also a lack of consistency in the reporting of δD of the non-exchangeable hydrogen (Wassenaar and Hobson 2000). However, the automation of hydrogen analyses will increase the standardization of the technique and allow for more cross-study comparisons in the future (Wassenaar and Hobson 2003).

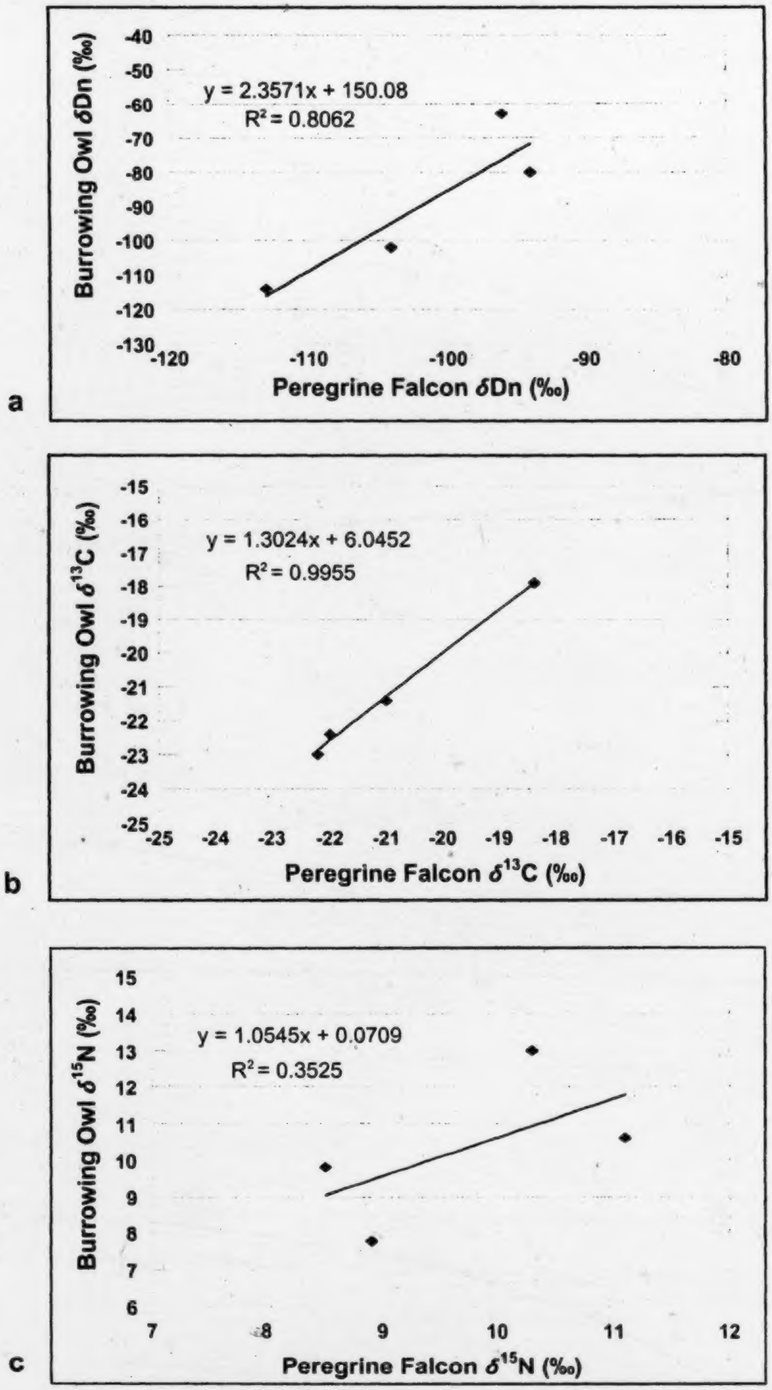


Figure 6-1. A comparison of isotope values of similar locations in the Peregrine Falcon and Burrowing Owl reference datasets.

Literature Cited

Erickson, G. L., R. Fyfe, R. Bromley, G. Holroyd, D. Mossop, B. Munro, R. Nero, C. Shank, and T. Weins. 1988. Anatum Peregrine Falcon recovery plan. Canadian Wildlife Service, Ottawa, ON. 52 pp.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N and S isotopic composition. Limnology and Oceanography 33:1182-1190.

Haug, E.A., B.A. Millsap, and M.S. Martell. 1993. Burrowing Owl (*Speotyto cunicularia*). *In:* A. Poole and F. Gill [Eds.], The Birds of North America, No. 61. Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue dependent stable-isotope models. Marine Ecology Progress Series 95:7-18.

Hobson, K.A. 2002. Science's Compass: Incredible journeys. Science 295:981-982.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using ^{13}C and ^{15}N analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K.A., K.P. McFarland, L.I. Wassenaar, C.C. Rimmer, and J.E. Goetz. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable-isotope analyses of feathers. Auk 118:16-23.

Kelly, J.F., V. Atudorei, Z.D. Sharp, and D.M Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. Oecologia 130:216-221.

Meehan, T.D., C.A. Lott, Z.D. Sharp, R.B. Smith, R.N. Rosenfield, A.C. Stewart, and R.K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. Condor 103:11-20.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochemica Cosmochemica Acta 48:1135-1140.

Rubenstein, D.R., C.P. Chamberlain, R.T. Holmes, M.P. Ayres, J.R. Waldbauer, G.R. Graves, and N.C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable-isotopes. Science 295:1062-1065.

Wassenaar, L.I. and K.A. Hobson. 2000. Improved method for determining the stable-hydrogen isotopic composition (δD) of complex organic materials of environmental interest. Environmental Science and Technology 34:2354-2360.

Wassenaar, L.I. and K.A. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39:211–217.

Appendix A

Stable Isotope Notation and Nomenclature

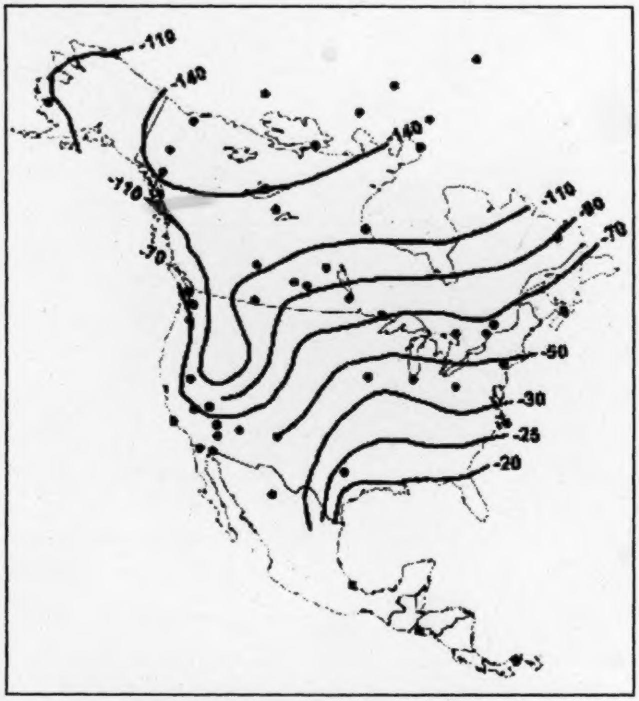
Stable isotope ratios of samples are expressed in δ (delta) notation according to the following formula:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where: X is the isotope in question (e.g. $\delta^{13}C$) and R is the isotopic ratio of the sample or standard (e.g. $^{13}C/^{12}C$). Carbon isotopic ratios ($\delta^{13}C$) are expressed relative to the PeeDee Belemite (PDB) international standard. Nitrogen isotopic ratios ($\delta^{15}N$) are expressed relative to atmospheric N_2. Hydrogen isotopic values are reported as δD values relative to the Vienna Standard Mean Ocean Water (VSMOW). **R**sample is the ratio found in the sample tissue. The result is the amount of heavy isotope within a tissue relative to that found in the standard. The relative amount of naturally occurring heavy isotopes is less than 1%. Therefore, final numbers are multiplied by a thousand and are presented in the per mil (‰) notation.

Appendix B

Hydrogen isotope patterns in precipitation across North America


-110
-140
-140
-110
-70
-110
-90
-70
-50
-30
-25
-20

Continental patterns of δD values in precipitation across North America (from Hobson and Wassenaar 1997).

Jason Duxbury
Department of Renewable Resources
4/42 Earth Sciences Bldg
University of Alberta
Edmonton, Alberta
T6G 2E3
CANADA

Our ref: EP/gIEH/1251

18th November 2003

Dear Jason Duxbury

Thank you for your correspondence requesting permission to reproduce the following material from our Journal in your thesis.

'Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope based maps for tracking migratory birds' by J M Duxbury, G L Holroyd and K Muehlenbachs, *Isotopes in Environmental and Health Sciences*, (2003) vol. 39 no. 3 pp 179-189

As you are one of the authors of the article, we will be pleased to grant entirely free permission on the condition that you acknowledge the original source of publication and insert a reference to the Journal's web site:

http://www.tandf.co.uk/journals/titles/10256016.html

Thank you for your interest in our Journal.

Yours sincerely

Elizabeth Potts
Permissions Administrator (UK) Journals
Elizabeth.Potts@tandf.co.uk